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REDUCTION IN PRODUCTIVITY OF MUSKRAT PELTS ON AN IOWA MARSH THROUGH DEPREDATIONS OF RED FOXES [1]

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INTRODUCTION

The muskrat (*Ondatra zibethicus*) (*2*)[2] constitutes a major economic resource in many parts of North America. Even in midwestern agricultural communities the income from the sale of pelts taken on superior muskrat marshes often has been equal to, or actually exceeded, monetary returns from farm crops and livestock raised on adjacent lands. In view of the decline of important fur bearers in recent years (*15*), it is not surprising that there should be a growing interest in muskrat management on a sounder production and cropping basis.

The muskrat is at times subject to conspicuous predation by certain types of flesh eaters, a fact which naturally arouses speculation as to how much damage may result and to what extent it may be averted through repressive measures against the predators. In Iowa, field researches begun in 1932 have demonstrated that the majority of muskrats known to have been killed by predatory enemies other than man or their own kind were victims of minks (*Mustela vison*), great horned owls (*Bubo virginianus*), and red foxes (*Vulpes regalis*). Analyses of mink and horned owl predation upon muskrat populations have already been reported (*6, pp. 191–192; 11; 13, pp. 792–793*); this paper records the data on red fox predation.

Although the foxes clearly have killed far fewer muskrats on the Iowa study areas than have the minks, fox predation, because of special aspects, may very conceivably have the greater economic significance. The distinction may be emphasized that intercompensatory or automatically adjusting trends in both reproductive and loss rates of the muskrats have served to nullify, in effect, most of the heavy as well as the light predation suffered (*9, p. 182; 10, pp. 166–167, 178–179; 11*). This means that as a rule the predation was borne by muskrats living under such disadvantages that they (or their numerical equivalents) were doomed anyway, if not from interspecific attack then from intraspecific, or from climatic emergencies or miscellaneous agencies. Fox predation, nevertheless, may not always be

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[2] Italic numbers in parentheses refer to literature cited, p. 147.

regarded merely as substituting one loss for another, with inconsequential differences in end results; and dissociation of its noncompensatory from its intercompensatory phases is a main objective of this writing.

THE GENERAL PICTURE OF RED FOX PREDATION UPON MUSKRATS

Preying by red foxes upon muskrats is variously mentioned in North American literature, and it was quite to be expected that introduction of the muskrat into Europe should have been followed by reports of its utilization by *Vulpes vulpes* (*26, pp. 38–39; 27, pp. 195–196*). In the eastern part of the United States, muskrats seem to occur particularly in the spring diet of *V. fulva* (*1, 14, 16, 20, 25*), and their remains may be well represented about the dens where young foxes are kept (*14, pp. 20–21; 25, p. 19*). Smith (*25, p. 19*), reporting on muskrats in Maryland, stated that ". . . practically all trappers regard foxes as serious pests on a marsh. On June 27, 1934, a fox den from which the old fox had recently removed her cubs was visited. Among the food remains were found the skulls and other bones of 12 adult muskrats." Investigations of the food habits of *V. fulva* and *V. regalis* in the North-Central States brought out little evidence of muskrats being taken during "normal" years except to some extent in spring (*3, pp. 20–25; 4, pp. 192–193; 17; 24*).

In the spring of 1934, 38 muskrat carcasses comprised 1.33 percent of 2,848 prey items recorded from 200 Iowa red fox dens, as compared with 2 carcasses, or 0.2 percent, of 1,010 items from 113 dens in 1933 (*5, p. 56*), but the increased severity of the 1934 predation may be attributed in large measure to exposure of muskrats by the spring drought of that year. "Normal" spring vulnerability of these animals to predators, including foxes, is usually distinct from drought vulnerability and seems mainly to relate to transient, unmated male muskrats, which are often handicapped not only by unfamiliarity with the terrain and inferiority of the living quarters available to them but also by their own restlessness and the intolerance displayed toward them by members of population groups already in established residence (*9, pp. 176, 178; 11, pp. 833–841*). The habitual spring wanderers observed in Iowa have been a biological surplus and thus highly susceptible to predation—indeed a surplus that has tended to be dissipated so completely by early summer that the presence or absence of foxes, minks, or any other kind of wild predators seemingly has had scant influence on its fate. This has been true whether the surplus males were in good or poor physical condition, formidable fighters or scrawny individuals dying from wounds of intraspecific harassment.

Murie (*19, table 1*) found muskrat remains in 45, or 5.8 percent, of 768 red fox droppings gathered on the Edwin S. George Reserve in Michigan from January to August 1934. Most of the muskrat representations were listed for the spring months, but the same author (*pp. 36–37*) explains that the marshes had little or no water in them during the winter and he suggests that the ". . . muskrat under conditions more favorable to its mode of life than those existing on the George Reserve would probably be less vulnerable to fox attack." His description of surface activities of the muskrats is indicative of drought vulnerability comparable to that observed in Iowa under extreme conditions (*7, 11*).

The water levels of Round and Mud Lakes, two neighboring marshes north of Ruthven, in northwestern Iowa, were very low in November 1936. The muskrat population of 450-acre Round Lake averaged about 1 per acre; that of a 300-acre section of Mud Lake, about 1⅔ per acre (7). The proportion of wanderers was much higher on Mud than on Round Lake,[3] and both marshes were being hunted over by foxes. A single fox scat examined from Round Lake contained muskrat remains, whereas none of eight from Mud Lake did. Round Lake also had water over much more of its bottom than Mud Lake, hence more of it had been inaccessible to hunting foxes up to the late fall freezing; on Mud Lake, nearly 100 acres (about 40 of which were occupied by muskrats) had been dry enough to permit movement by foxes almost everywhere since midautumn. The Mud Lake foxes simply did not respond to the pronounced vulnerability of the muskrats.

Later in the winter, intensive studies of a drought crisis were carried on at Little Wall Lake, a 230-acre marsh south of Jewell, in central Iowa. The muskrat population entering the winter was but a remnant of what it had been months previously, and was calculated at about 40 individuals on about 100 acres still occupied (7). The marsh was entirely depopulated of muskrats by early February, and some data were acquired concerning the fate of about three-fourths of the animals that had entered the winter. The diets of local minks were made up to a substantial extent of muskrats, both of mink-killed victims and of carcasses of those dying from intraspecific wounds, hunger, and cold; fox "sign" was conspicuous on the dry marsh bed, but these predators did not appear to be especially interested in the muskrats. A fox was once noted (December 8) to have defecated on a muskrat that had died of muskrat-inflicted wounds, and, later (February 11), a fox scavenged upon a carcass of which parts had been dug out of the snow.

In the spring of 1937, Little Wall Lake was partially repopulated, 7 breeding females and associated males moving in from surrounding habitats to station themselves in about 90 acres of marsh habitable at the time. These were known to have given birth to 13 litters, totaling well over 100 young.[4] The marsh went dry in later summer and had only a remnant population by November, 16 individuals, as reported by trappers. Yet, aside from fragments of a muskrat that had probably died in the winter, no remains of muskrats were detected amid the prey debris littered about a series of marsh-edge trails and den holes used until late summer by a family of foxes.

Approximately two-fifths of the bottom of Cheever Lake, a 282-acre marsh area near Estherville in northwestern Iowa, was exposed by drought in the late fall of 1939. Muskrat densities on the wet marsh were high—1,680 being the figure arrived at on the basis of generally accurate data. In addition, about 85 animals were determined to be resident, though precariously situated, in dry habitats. Twenty-five carcasses, known to be chiefly those of victims of intraspecific strife and minks, were found between September 28 and November 19, and only 1 of 6 live specimens collected on shore for examination was

[3] A deliberate effort to collect all wanderers on Round Lake yielded 4 live specimens, 1 dead, and gave indications of at least 1 escaping; the private fur catch from the completely exposed marsh bottom of Mud Lake was 42 pelts.

[4] Six of these litters were plainly complete when handled and averaged 8⅔ young.

without the strife wounds typically borne by drought-evicted wanderers at this time of year. Foxes hunted in accessible parts of the marsh, but no evidence was seen either of their scavenging upon carcasses of muskrats or hunting live ones. Conditions at Cheever Lake grew worse in 1940, and the last of the surface water disappeared on October 22, which resulted in severe mortality and final abandonment by nearly all of a remnant population estimated at about 200; foxes hunted even in the center of the lake bed but without leaving any observed evidence of killing or eating muskrats. In contrast, the minks responded conspicuously to the vulnerability of large numbers of muskrats brought about by the two autumnal drought crises (*11, pp. 859–865*).

From the foregoing review it is apparent that definite instances of red foxes preying heavily upon muskrats are not abundantly recorded [5]; hence a situation studied in 1940 at Wall Lake, a 935-acre marsh north of Blairsburg, in north-central Iowa, merits discussion in some detail. Preliminary references to predator-prey relationships on this marsh have been made in connection with the analysis of the mink predation (*11*).

METHODS OF INVESTIGATION

A regular program of field research on the muskrats of Wall Lake was begun by the senior author in May 1939. The standard investigative procedure was to try to locate all habitations of females with young [6] and thus to determine the foci of breeding "territories," to obtain data on size of litters and sexes and ages of individuals by techniques previously demonstrated (*8*), to mark the litter members by tagging (*12*) and toe clipping,[7] and, later, to obtain all possible data on behavior and mortality of the population until winter. When feasible, efforts were made to obtain for post-mortem examination an adequate number of specimens in November and December, the time of most fur trapping for Iowa muskrats. From these specimens, information on sex and age ratios, growth and developmental rates, numbers and comparative freshness of placental scars in the uteri of mature females, etc., were sought for correlation with the results of the preceding warm weather studies.

In 1940 the junior author began participation in the Wall Lake investigation, and thereafter the work was carried on jointly, each person assuming responsibility for data acquired for his own project. Hunting methods and related behavior of the foxes were deduced from tracks in the mud or peat bottom of the marsh, digging and trail "sign," and the appearance of prey remains. Scats of unquestionably fox origin were gathered, dated as closely as the evidence permitted, and finally examined in the laboratory with the aid of reference specimens.[8]

[5] Pancoast (22) ascribes tremendous losses to red foxes on New Jersey muskrat marshes, but, while the writers do not doubt that much evidence of killing was observed, reductions in trapping yields to one-fourth or less of "normal" are not, in view of apparent variables, necessarily chargeable solely, or even largely, to fox predation.

[6] This task was simplified by the fact that fewer than 50 acres were then habitable for the species because of a low water stage; the resulting wide, flat shore margin, not being conducive to the maintenance of bank burrows, forced the females to keep their litters in lodges and nests where they could be easily reached by hand.

[7] ASHBROOK, F. G. MARKING WILD ANIMALS FOR IDENTIFICATION. U. S. Dept. Agr. Wildlife Res. and Mangt. Leaflet BS–57, 3 pp., illus. [Processed.]

[8] Acknowledgment for help in identifying fecal contents is due particularly to Harry Harrison and Ray Erickson, of Iowa State College, and Jason R. Swallen of the Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture, as well as to the Patuxent Food Habits Laboratory of the Fish and Wildlife Service.

It has long been recognized that neither fecal analysis nor any one method of studying food habits of foxes, when used alone, is free from disadvantages (*4*, *23*), so the practice in this investigation has been to seek data by all practicable means and to try to derive conclusions from the total evidence available. Actually, the fox droppings did prove to be the best single source of information, but uneaten prey debris and other "sign" also contributed much of value; and the resulting ecological picture, though in many ways incomplete, can be said to reflect trends in predator-prey relationships.

There is no reason to believe that the presence of the investigators materially influenced the behavior either of the foxes or the muskrats, or of other wild animals importantly involved. The foxes showed a tendency to avoid parts of the dry marsh frequented by farm dogs but appeared tolerant of the research activities, which, of course, were conducted in ways intended to be least disturbing.

THE WALL LAKE CASE HISTORY

The Wall Lake muskrat population was calculated at 275 to 280 individuals on 34 acres of marsh occupied early in the winter of 1939–40. About 15 of the 34 acres constituted excellent wet marsh habitat, and here a population of over 200 was judged to have wintered with little loss. Elsewhere on the marsh, shallow water and continued dry weather afforded the muskrats little or no winter protection, and mortality from dogs, minks, hunger, and cold was pronounced. Survival figures of 18 to 22 out of 55 to 60 were arrived at for the inferior habitat, which would give a total survival of something over 200 muskrats for the marsh.

By the spring of 1940 there was sufficient water to bring the marsh level back to about where it had been in the late fall of 1939. Six tracts of fairly open water ranged in size from approximately 1 to 4 acres and were surrounded by dense stands of emergent vegetation, mainly bulrushes (*Scirpus* spp.), cattail (*Typha latifolia*), and reed (*Phragmites communis*).

The first careful inventory of "territories" in 1940 was made on May 30 and 31—at which time Iowa muskrats are usually in permanent summer residence—and the data procured then and later indicated an initial density of 41 to 46 females and possibly a somewhat larger number of males. Eleven of the females had their "territories" on 10 acres of the shallower parts of the marsh, and the 30 to 35 others had settled on the wetter 24 acres of the occupied area.

The breeding season was favorable for deep and shallow marsh muskrats alike throughout the first 3 weeks of June. Four of 30 mink scats that could be satisfactorily assigned to early May contained muskrat remains but these were probably all of the same victim; there were no representations of muskrat in 106 scats from late May and June. The maximum number of young muskrats present at any one time was estimated at between 500 and 700. Sixty-one young muskrats in 15 litters and a litter of 5 young minks were marked, but, of these only a single toe-clipped muskrat was subsequently recovered.[9]

[9] The writers' records show that 134, or 19.5 percent, of 686 Iowa muskrats yielded data after marking and that, under conditions favorable for study, it might be expected that about 30 percent of the individuals marked would be recovered.

By June 20, the marsh bottom of about half of the 34-acre occupied area was exposed except for puddles and water in the entrances of the lodges. Friction between adult muskrats was observed on one of the drier tracts, and the situation was becoming critical for an increasing number of residents. The species had not as yet suffered unusual mortality, however, although foxes were displaying interest in two sets of lodges. This place, where the attention of the foxes was attracted by the shallow-water muskrats, was near the east-central shore, across the marsh from the apparent sites of the spring fox dens. The foxes limited their explorations to areas of bottom firm enough to prevent their feet from sinking more than about an inch. Minks frequented mainly the deeper marsh, where they were living almost entirely upon coots (*Fulica americana*); no muskrat remains were found in 30 of their scats deposited during the middle of June.

A local 3-inch rain on the night of June 22 had made little perceptible difference by June 24, and by June 26 the appearance of the marsh was much as it had been just before the rain. Drought-exposed muskrats (calculated at 30 to 50 individuals, in the ratio of about 3 young to each adult) were foraging in the vegetation near the lodges and extending their diggings. Foxes, while including cottontail rabbit (*Sylvilagus floridanus*) and miscellaneous beetles in their diet, were now taking full advantage of the muskrats, all of 6 scats containing remains of young animals 6 to 10 weeks of age.

During July the drought increased in severity and dried out the habitats of between 50 and 200 muskrats. By the early part of the month, the foxes, plainly hunting as a family group and systematically working muskrat feeding grounds in the vicinity of newly exposed lodges, had caught nearly all the young muskrats in the tract that first went dry. They next worked southward in the marsh, keeping close to the edge of the receding water (often going so close as to sink 2 or 3 inches in the mud), and by the end of the month had caught practically all except the adult muskrats on at least 20 acres of marsh. Three carcasses of adult muskrats were located but these were more likely victims of intraspecific strife than of predation; fragmentary carcasses of 6 young between 5 weeks and 2 months of age, probably or certainly killed by foxes, were examined. Forty-five of 47 fox scats contained muskrat remains, mostly of animals between 2 and 3 months old. Minks seemingly avoided the places heavily hunted by the foxes and were not known to have killed muskrats in any place where surface water remained in the lodge entrances. The minks did hunt in a dry corner of the marsh that, as yet, had not been exploited by the foxes. Four of eight mink scats contained remains of about the same age classes of young muskrats as the fox prey.

Fox diets during July reflected highly opportunistic hunting. In addition to the muskrats, other inhabitants of marshlands were taken, especially beetles. Of 47 fox scats examined, 19 contained avian remains, those recognized being mainly of coot and duck (Anatidae). Garter snakes (*Thamnophis*) were abundant on the dry marsh bottom, and were fed upon, as were crayfishes (*Cambarus*). A huge snapping turtle (*Chelydra serpentina*) had been dug out of the mud and most of its flesh had been eaten; turtle remains were found in 1

scat. Single representations of cottontail and shrew (*Sorex cinereus*) and 2 of young meadow mouse (*Microtus*) were present in the 47 fecal samples.

In late July, the fox family (the "sign" indicated a group of four animals) was centering its activity in the south-central part of the marsh. Hunting techniques, as revealed by tracks, seemed to entail a definite system of maneuvers, some foxes stationing themselves beside the trails between muskrat lodges and feeding grounds while others circled about. It is probable that the effectiveness of the system resulted not so much from genuine teamwork as from the astuteness of old foxes in waiting near places where alarmed young muskrats would be apt to run. No evidence of digging into muskrat-occupied lodges or burrows was disclosed, although a nest of incompletely hatched snapping turtle eggs was dug out of the top of an old lodge.

By the beginning of August the water level was so low that a muskrat population of possibly 250, with a ratio of about 2 young to each adult, had been exposed. Only 1 carcass of a fox victim (a young animal of about 3 months) was found, but 18 of 20 fox scats deposited up to the middle of the month contained remains of muskrats, chiefly of young of 2 months to subadults of 3½ to 4 months. There was still no evidence of foxes successfully catching adult muskrats, though the minks were killing some in the long-exposed tracts that the foxes had virtually depopulated of young and then abandoned. Muskrat representations (including 3 of adults) were listed for 4 of 7 mink scats picked up in such places, and 20 scats from wetter habitats had remains of young or subadults in 3.

By August 6 rains filled the deeper part of the marsh to a depth of several inches and by mid-August the latter habitat (which not only had the highest density of muskrats but also had been the last to go dry) was well reflooded. With this reflooding, the foxes gradually discontinued their lowland hunting and spent much of their time along the southwest shore of the marsh and on the adjoining cultivated land. A trail of about 200 yards extending through dense vegetation from shore to the west fringe of the wet area showed heavy passage, and there was evidence of foxes using old lodges as beds. Although one muskrat was known to have spent some time in a cornfield that was the principal headquarters of the foxes in late August, there were probably no more than a dozen vulnerably situated muskrats about the entire marsh at this time, and these seemed to be transients, both in the marsh and on high ground. Muskrat representations were found in 2 of 20 mink scats and in 3 of 11 fox scats deposited from late August to the middle of September, and a shift in dietary trends of the foxes from muskrats to rabbits, mice, and birds became apparent.

After the middle of September, the foxes moved northward into the vicinity of what were believed to have been their former breeding dens, thus completing during the summer season a clockwise circuit with a radius of about a half mile; the total area hunted over during this period was certainly not much larger than a square mile.

By September 25 the marsh was again going dry, and by the middle of October the bottom was fully exposed. Muskrat remains were

found in 4 of 11 mink scats but in none of 6 fox scats. The foxes no longer spent much time in the marsh, despite the fact that a population of over 200 muskrats in ratios of 1.9 young to each adult and 3.1 young to each adult female lived vulnerably in habitats with which the foxes were familiar.

Trapping by the public in November practically annihilated the muskrats, the catch being 197. Of these, the carcasses of 105 were examined. There was evidence of a few trap cripples wandering over the frozen marsh after the trapping ceased, but no muskrat representations were found in 145 fox scats deposited from October 1940 to early March 1941.

The marsh was restocked naturally with muskrats to a limited extent during the 1941 spring dispersal of that species from stream habitats in which winter survival had been better, and the summer population of adults was ascertained to be 5 pairs (or equivalent) and 1 unmated or nonbreeding female. During the early stages of the dispersal in the first half of March, a considerable number doubtless moved about the countryside. On March 12, a freshly killed, maturing male muskrat was found at a den at which newly born fox pups were kept, and 1 scat passed between March 16 and March 20 was of muskrat remains; since the first carcass had been taken to the laboratory before the foxes had eaten of it, the fecal representation was of a different victim. No other muskrat remains were found in the rest of a collection of 194 scats (51 of these were pup scats) deposited from the middle of March through April. The foxes subsisted mainly through the fall to spring period of 1940–41 on rabbits, mice, and birds.

The fox pups were judged to be 6 or 7 weeks old by May and, by the middle of the month, were penetrating about 100 feet into the vegetation at the west-central side of the marsh. By this time, several sets of more or less neighboring holes had been used as den headquarters; by June 10, the fox family (there were at least four young) seemed to be ranging free from the dens and, by the end of the month, had definitely abandoned them.

August 1941 brought another drought to the Wall Lake muskrats, but they were relieved by rains after about 3 weeks of exposure. No tracks of foxes were seen in the dry central parts of the marsh, however, and no muskrat remains were found in 555 scats deposited from May through August.

No notable mortality was suffered by the muskrats in the fall until the local population was once more virtually annihilated by public trapping. The sex and age ratios of the carcasses obtained from trappers in December suggested a rate of increase of only 4.6 young per breeding female, although the average of the season's placental scars was about 30—which represents a typically severe reduction in young for the length of time that they were exposed by drought.

No sign of family association of foxes was seen after early September and, by early October, the evidence of foxes noticed on the area was northeast of the marsh. Thirty-three scats collected from September 1941 to January 1942 showed the usual diet of upland vertebrates.

ANALYSIS OF THE FOX PREDATION UPON THE WALL LAKE MUSKRATS

From previous and contemporaneous investigations, one would expect a great deal of flexibility in general predator-prey relationships in the north-central part of the United States (*11; 13*). Most predatory higher vertebrates studied in this region have shown slight evidence of obligatory dependence upon any one or any group of prey species, even of species usually classed as staple prey. It is, therefore, unlikely that shortage of a prey species often served to force a predator into any particular diet, although a versatile predator no longer able to exploit its customary prey would naturally turn to one or more of the other species remaining available.

Availability of prey, relative or absolute, appears to be of outstanding importance in determining the food habits of the common raptorial birds and carnivores, but responses to changing availability may also be conditioned by other factors. Lack of responsiveness of one predator to increased availability of a given prey species may or may not be accompanied by greater response on the part of other predators. The point to be recognized is that, irrespective of the fundamentally mechanical aspects of predation, the role of chance and the differences in adaptability, experience, hunting routines, and predilections of the predators may be sufficiently influential to make attempts at very detailed cause-and-effect appraisals impractical, if not downright unreliable. And a participant capable of as much individuality as the red fox adds more than usual variability to the predator-prey equation with which we are here concerned.

The factors governing availability of prey to general-feeding predators may be exceedingly complex in analysis, but fall into a number of fairly clearly-defined categories. Broadly, the more abundant a species, the greater is the likelihood of its being preyed upon, especially in its immature stages (*18*). Among vertebrate species showing "territorial" intolerance (*21*), thresholds of security often exist, and populations in excess of these thresholds may be notably vulnerable to predation (*11, 13*). Anything, in short, that promotes disharmony or instability in vertebrate populations increases vulnerability to predatory enemies.

The Wall Lake case history depicts many responses of foxes to changes in the availability of foods. Rabbits and mice were the dietary staples; for one reason or another they almost always continued to be available at all seasons to avian and mammalian predators generally, as well as to the foxes. When the sudden Armistice Day blizzard of 1940 killed immense numbers of late-moving, red-winged blackbirds (*Agelaius phoeniceus*), the foxes immediately responded to this source of convenient and acceptable food. An apparent overpopulation of pheasants (*Phasianus colchicus torquatus*) massed near a cornfield in late November and December 1940 was not overlooked, nor were field-ranging chickens from farmyards in the summer of 1941. During the drought of 1940, as indicated, even the marsh-dwelling turtles suffered predation from foxes.

The predation upon the drought-exposed muskrats, with some differences, was much according to previously observed patterns. The

differences, nevertheless, were in many ways significant because of the specialized and effective hunting techniques of the foxes and the combination of variables arising from weather and unknown factors.

Presumably, the foxes were going to the water's edge to drink in June 1940 when they were attracted by a group of land-active, insecure muskrats. It might not be demonstrably correct to say that the latter were prey truly preferred by the foxes above all others but, at any rate, they became objects of unquestionably deliberate search. Furthermore, the muskrats of the shallow-water zones had suffered, through the enterprise of the foxes in 1940, nearly complete loss of their season's young, days or even weeks ahead of any ordinary schedule of drought mortality.

Had it not been for the fox depredations, the breaking of the drought by the August rains would either have averted the greater part of the midsummer losses or would have resulted in something of a postponement until the recurrence of the drought in the fall. It is conceded that many of the muskrats eliminated in the summer by the foxes would surely have died anyway from mink predation, intraspecific strife, etc., during the fall crisis, but, taking into consideration as well as we can the intercompensations indicated by the data, it may be concluded that an actual uncompensated lowering in productivity of between 50 and 100 muskrats must be charged to the foxes (*11*, *p. 881*).

This would mean, on the basis of the average of $1.21 received by Iowa trappers for 1940–41 muskrat pelts,[10] a net loss possibly exceeding $100.00 in trappers' income from the marsh—possibly a reduction of about 25 percent in the value of the fur returns. It is not believed that the predation by foxes or other wild animals had depletive influence on the breeding stock of the following spring, for, under the circumstances, human exploitation would probably have been as annihilative if there had been no "natural" predators in the vicinity.[11]

In 1941, the foxes, which there is some reason to believe included the original pair of adults, caught about as many of the spring-dispersing muskrats as they could be expected to encounter at random; on the other hand, they apparently did not happen to hunt in those places where the muskrats were again exposed by drought, so the predation sequences of 1940 were not repeated.

SUMMARY

In the summer of 1940 a study was made of an exceptionally drastic predation by red foxes upon the drought-exposed muskrat population of Wall Lake, a marsh in north-central Iowa. The severity of the crises confronting the muskrats doubtless would have resulted in heavy losses in the absence of the foxes, but to the specialized and effective hunting techniques used by the latter may be ascribed a reduction in muskrat numbers that seemed to a considerable extent noncompensatory. A possible net decrease through the fox depredations of about 25 percent of the trappers' income from the marsh is indicated by the data obtained.

[10] IOWA STATE CONSERVATION COMMISSION. NUMBER AND VALUE OF FURS TAKEN IN IOWA, 1940–41 SEASON. Iowa State Conserv. Comm. 1941. [Processed.]

[11] Readers interested in the problem of overtrapping as it relates to muskrat management may consult an earlier paper (*9*).

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RANGE OF SOIL-MOISTURE PERCENTAGES THROUGH WHICH PLANTS UNDERGO PERMANENT WILTING IN SOME SOILS FROM SEMIARID IRRIGATED AREAS[1]

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INTRODUCTION

It has long been known that the wilting coefficient, or wilting point, of a soil does not represent the lower limit of soil moisture available to plants but rather the approximate lower limit available for growth (*6*).[3] Some writers, however, have used the term rather loosely to refer to the percentage of nonavailable moisture, possibly on the assumption that the amount of moisture available at moisture percentages below the wilting point is so small as to be of no practical significance.

Alway (*1*), Batchelor and Reed (*3*), and others have reported finding soil under deep-rooted trees or shrubs at moisture percentages well below the wilting coefficient and in some cases at about the hygroscopic coefficient. These writers pointed out the significance of the moisture below the wilting coefficient in the maintenance of life in these plants during periods of prolonged drought, and Batchelor and Reed proposed that, since the wilting coefficient does not represent the lower limit of available moisture, the hygroscopic coefficient be used as the reference value for expressing the relative wetness of a soil as related to plant behavior. While the hygroscopic coefficient, in the sense in which this term was employed, is no longer in general use as a soil-moisture constant, Batchelor and Reed's contention that a soil-moisture constant, approximately equivalent to the nonavailable soil-moisture percentage, is needed, is nevertheless a pertinent one.

In recent investigations of the response of citrus trees to various soil-moisture conditions (*10*), it was found that the water deficit of trees in the field was related not only to the proportion of soil in the root zone that was reduced to the first permanent wilting point, but also to the extent to which the moisture content of the drier parts of the soil in the root zone was reduced into the wilting range.

The wilting range is the range in soil-moisture percentages in which plants undergo progressive permanent, or irreversible, wilting, from

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[3] Italic numbers in parentheses refer to Literature Cited, p. 169.

wilting of the oldest leaves to complete wilting of all the leaves. The lower end of this range has been termed the "ultimate wilting point." In this paper wilting is called permanent if turgor is not regained by the uninjured leaves when the plant is kept in an approximately saturated atmosphere in a dark humid chamber for 14 to 16 hours.

The terms "wilting range" and "ultimate wilting point" were introduced by Taylor, et al. (*17*) to describe the soil-moisture conditions in plots of native California shrubs, where they found that the soil-moisture content, to a depth of 6 feet or more, was appreciably below the first permanent wilting point at the end of the dry season. They defined the wilting range as the range in moisture content of the soil between the wilting coefficient and the ultimate wilting point, and the ultimate wilting point as the moisture content at which all the leaves remain completely wilted in a humid atmosphere. That is, the ultimate wilting point represents approximately the lower limit of the range of soil-moisture percentages in which plants are able to maintain life, though at this stage many of the leaves and probably some of the roots are dead. Even at the ultimate wilting point a small amount of soil moisture is, of course, still available to living tissue, and it might be supposed that the logical end point in determining the available moisture held by a soil would be the soil-moisture percentage at which the process of dying had just been completed.

Such determinations would, however, be time consuming, and the time when death was complete would be uncertain; furthermore the percentage of moisture at the death point is numerically practically the same as that at the ultimate wilting point, though, of course, at such low moisture percentages a small change in moisture represents a relatively large change in the vapor pressure or moisture tension of the soil.

Since the first permanent wilting point, or wilting coefficient, corresponds to approximately the soil-moisture percentage at which elongation ceases, and since the ultimate wilting point represents practically the lower limit of soil moisture that can be utilized by the plant in maintaining life, it would seem that in studies dealing primarily with the response of plants to soil-moisture deficiency these two reference values should provide adequate bases for comparison with most soil-moisture conditions encountered.

The wilting range, as here defined, has been reported for only a few soils (*10*, *17*). Since more general information was needed in connection with irrigation experiments, it seemed desirable to determine the wilting range of a large number of soil types varying widely in texture and other characteristics.

METHODS

Samples of about 80 soils, representing about 50 soil types as shown on soil survey maps of several areas of southern California, were collected for the study. With few exceptions the soil samples were taken from the top foot of soil, and most of them were from cultivated, irrigated orchards or fields. A few samples were from uncultivated desert lands or brushlands. The samples were air-dried and screened through a 2-mm. round-hole screen.

Moisture-equivalent determinations were carried out with standard apparatus, and the precautions recommended by Veihmeyer et al. (*19*) were observed. Four samples of each soil were run, and the average was taken as the moisture equivalent. In a few instances in which the four samples showed unsatisfactory agreement the determinations were repeated.

The wilting range determinations were made during the period from September 1940 to May 1941 at Pomona, Calif. The procedure for determining the wilting range is simple, but certain precautions were found to be necessary in order to obtain reliable results. The method employed proved to be convenient, economical of time, and reasonably reliable. Ten cultures with each soil sample, 5 for the determination of first permanent wilting and 5 for the determination of ultimate wilting, were run. The plant containers used were pint, compression-top cans, with ¾-inch holes punched in the centers of the covers. Four or five hundred grams of soil, depending upon the volume weight, was weighed into each can. Weighings were made on a spring food balance of 1-kg. capacity, and the groups of 10 cultures were placed on flat trays on the greenhouse bench. Russian Giant sunflower (*Helianthus annuus* L.) seedlings which had just shed the seed coats were transferred from flats of sand to the soil culture, 1 plant to a can.

It was found that frequently plant growth was poor unless care was taken to maintain ample soil pore space in the cultures. Jarring the cans after filling them caused appreciable settling of both dry and wet soil; so when the seedlings were transplanted to the cans, all the soil was poured out of the culture can into another container and then poured back into the can through a funnel while the plant was centered in the can by means of a small planting guide shown in figure 1, *A*. The roots of the seedlings were dipped into a soil suspension just before they were planted. This coating of the roots with a thin layer of fine soil at planting hastened recovery from transplanting. This improvement in recovery must have resulted either from protecting the absorbing surfaces from momentary drying or from improving contact between soil and roots, since it was found that regardless of treatment, the old root tips did not resume growth after transplanting but that new root growth arose from lateral root initials, which appeared about 2 days after transplanting.

After the seedlings were planted, the surface of the soil in the can was covered by a layer of absorbent cotton and the lid was fitted in place; then the culture was placed on the spring balance, and the weight of water required to wet the cotton, plus the calculated amount required to raise the moisture content of the soil to field capacity, was added from an overhead supply bottle. The cotton was placed on the soil surface to protect it from being puddled when water was added and to encourage the development of roots in the surface layer of soil. To loams and clays, nitrogen (50 to 100 parts per million of soil) was added in the water at planting and a small amount of monopotassium phosphate (KH_2PO_4) was mixed with the dry soil before planting. The sands were watered at planting with a complete nutrient solution. The first set of cultures run were fertilized with nitrogen only, and determinations on some of these soils had to be repeated because the lower leaves were severely affected by symptoms of malnutrition and failed to show normal recovery after temporary

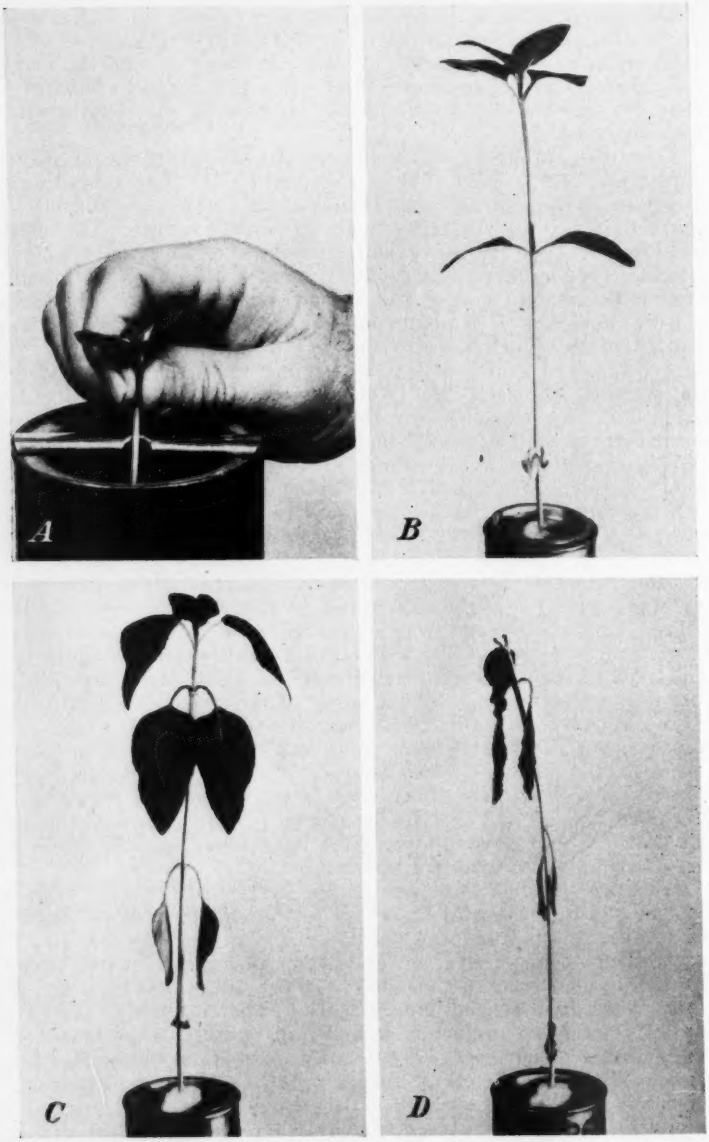

FIGURE 1.—*A*, Transplanting seedling to culture can; *B*, plant that had recovered turgor in the humid chamber after being wilted; *C*, plant at first permanent wilting point; *D*, plant at ultimate wilting point.

wilting. For a day after planting, the cultures were protected by a cloth shade, and then they were grown in full sun until the third pair of leaves had reached almost full size. Whenever some of the plants of a group in the same soil showed temporary wilting, water was added in sufficient quantity to bring the soil up to the estimated weight at field capacity, allowance being made for the increasing weight of the plants in estimating the quantity of water needed. When the third pair of leaves was almost fully developed, the soil was wetted to the estimated field capacity, the lid opening around the stem was closed with cotton, and watering was discontinued. As soon as cultures showed temporary wilting of the first pairs of leaves, they were placed under a cloth shelter, where they usually recovered turgor unless the leaves had been injured by fungus infection or malnutrition.

The lowest pair of leaves of a plant inadvertently left in full sun until several pairs were badly wilted usually showed injury and failed to recover turgor. Such plants could not be used for determining the first permanent wilting point.

When the lowest one or two pairs of leaves of cultures used for determining the first permanent wilting point wilted under the cloth shelter, the cultures were transferred to a dark humid chamber. High humidity was insured by exposing a large water surface in the chamber; in addition, just before the chamber was closed, the air was filled with a fine mist from a hand sprayer. As the plants recovered turgor, they were returned to the cloth shelter. This procedure of transferring the cultures back and forth from cloth shelter to humid chamber was continued until the basal pair of true leaves failed to recover after being in the humid chamber overnight. At this stage the tips of the second pair of leaves usually showed partial loss of turgor and drooped slightly. During the course of this process the time required under the cloth shelter before temporary wilting was induced gradually shortened until finally only a few minutes were required, and conversely the time required for recovery increased until finally recovery failed to occur within the overnight period of 14 to 16 hours. Since large numbers of plants can be transferred at one time, the labor involved in handling cultures in this manner is not prohibitive. The appearance of typical plants after recovery from temporary wilting and at the first permanent wilting point is shown in figure 1, *B* and *C*.

After the cultures used for determinations of the first permanent wilting point were watered for the last time, measurements of the stems were made early each morning with a ruler fitted with a sliding sidearm which could be brought into firm contact with the terminal growing point. Stem length was measured with an error of only about 1 mm. It was found that cessation of stem elongation coincides approximately with first permanent wilting as judged by the condition of the basal pair of leaves of normal plants. There was, however, some variability; some vigorously vegetative plants continued to elongate several millimeters a day for 1 or 2 days after the lower leaves were judged to be flaccid at the end of the 14- to 16-hour period in the humid chamber. Since, however, this rate of growth was very low as compared with the normal rate when the cultures were first sealed, approximate cessation of stem elongation was used as a secondary

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criterion of first permanent wilting and was especially useful with plants that had suffered some injury of the lower leaves but were not so badly injured as to be considered unsuitable for use.

The cultures used for determining the ultimate wilting point were left under the cloth shelter until the apical leaves were badly wilted. Unless the apical leaves are severely wilted, it is difficult to tell whether they show recovery in the humid chamber. At this stage the stems were frequently flattened and distorted and the older leaves were dead. When placed in the humid chamber they never showed more than very slight signs of recovery of even the apical leaves. The appearance of a typical plant at the ultimate wilting point is shown in figure 1, *D*. At the ultimate wilting point the terminal one or two pairs of leaves, the terminal growing point, and at least some of the axillary buds are alive and the plant will resume growth if the soil is wetted.

When the plants were judged to be at the first permanent wilting point or at the ultimate wilting point, they were pulled out of the soil so that the largest roots were removed. The top layer (about one-half inch) of soil, in which root concentration was usually low, was removed and discarded. The soil from the upper and lower halves of the culture cans was sampled separately. The moisture content, determined as loss under drying at 105° C., is expressed as percentage of dry weight. A comparison of the values for the two samples served as a convenient check on possible errors in manipulations or calculations, but the average of the two was taken as the moisture content of the culture, and the average of the five cultures was taken as the moisture percentage at the first permanent or at the ultimate wilting point. The moisture content of the soil from the lower halves of the cultures was usually 0.1 to 0.3 percent higher than that from the upper halves. This difference may have resulted from differences in root concentration, soil temperature, salt concentration, or loss by evaporation, but the cause was not determined.

The widest variations between the moisture percentages of the five cultures of a sample at the first permanent wilting point or at the ultimate wilting point ranged from about 0.3 in sands to as much as 2.1 in the heaviest clay. These variations resulted in part from variations in judgment of the several workers who handled the cultures and in part from unavoidable variations in severity of wilting before the plants were placed in the humid chamber for the last time. Slight variation may be expected also as a result of variability in the amount of mechanical tissue in plants grown under different conditions of nutrition, water supply, temperature, and other environmental factors.

In the literature wilting-point values are sometimes reported to hundredths of a percent of moisture, and usually the probable or standard errors reported are small. Perhaps such data imply that the methods used in wilting-point determinations lend themselves to greater precision and reproducibility than may actually be the case. It is to be expected that variations between individual cultures of one soil run at the same time by one worker will be small, but over a period of several months or years an individual worker's notion of what the plant looks like at some selected stage of wilting, as first permanent wilting or ultimate wilting, may vary considerably unless some well-

defined criteria are established for judging when the selected stage has been reached, and it is almost certain that the stage of wilting classed as permanent wilt has varied widely as judged by different workers in widely separated laboratories.

To obtain an indication of the variability which might be expected in wilting points run on the same sample of soil at different times, cultures from a large sample of clay loam were run through the usual procedure in the fall, winter, and spring along with other soils, so that only the usual care would be given them. The average values obtained for first permanent wilting point in fall, winter, and spring were, respectively, 19.9, 20.2, 20.3; and for ultimate wilting point, 17.3, 16.9, 17.0. The difference between the extremes in each case was 0.4 percent. That rather consistent results may be obtained in routine wilting-point determinations by the procedure described was demonstrated by the results obtained on samples from 12 field plots on a relatively uniform clay loam. Each sample was an unscreened composite of eight 4-inch auger borings distributed uniformly over each of the plots, which were about 160 feet long and 24 feet wide. The first permanent wilting points of the 12 samples ranged from 20.3 to 21.9, and the moisture equivalent ranged from 32.7 to 36.1. In routine field work the average value of first wilting point or ultimate wilting point for these plots might be used for any one of the plots without serious error.

The precautions found to be helpful in obtaining reliable first permanent wilting points may be summarized as follows:

(1) Good root growth and distribution should be obtained by maintaining ample pore spaces in the soil and avoiding wetting the soil far above field capacity.

(2) Vigorous and healthy plants should be obtained by maintaining favorable nutrition, preventing infection by fungi, and avoiding overheating of the soil in culture cans exposed to full sunlight.

(3) When the plants wilt, they should be placed in the humid chamber before excessive desiccation causes injury to the lower leaves.

(4) Daily measurements of stem elongation should be made as a supplementary indication of first permanent wilting. Basal leaves that have become senescent or have been injured, even though not showing obvious signs of injury, may fail to recover when the plant is still receiving enough water to cause appreciable growth. Plants elongating at a rate of more than about 10 or 15 percent of the rate maintained during the first 1 or 2 days after the final watering should probably not be considered as permanently wilted.

RESULTS

PLANT RESPONSE TO DECREASING SOIL MOISTURE

In general, the daily rate of stem elongation decreased soon after the cultures were sealed and watering was discontinued, but no definite conclusions as to the relation between growth rate and soil moisture above the wilting range can be made, because as soon as temporary wilting occurred the plants were placed in partial shade and part of the time in a dark humid chamber. It is clear, however, that even under these conditions elongation had almost or entirely ceased at the first permanent wilting point. Growth rate curves typical of the plants grown in soils of different textures ranging from sand to clay

are shown in figure 2. Measurements of stem elongation were also made on a number of plants used in determining the ultimate wilting point. These plants were placed under the cloth shelter when they first became temporarily wilted, but were not placed in the humid chamber until all the leaves were severely wilted. Elongation had approximately ceased when the basal leaves remained wilted overnight, and the stems, because of water loss, decreased in length before the ultimate wilting point was reached.

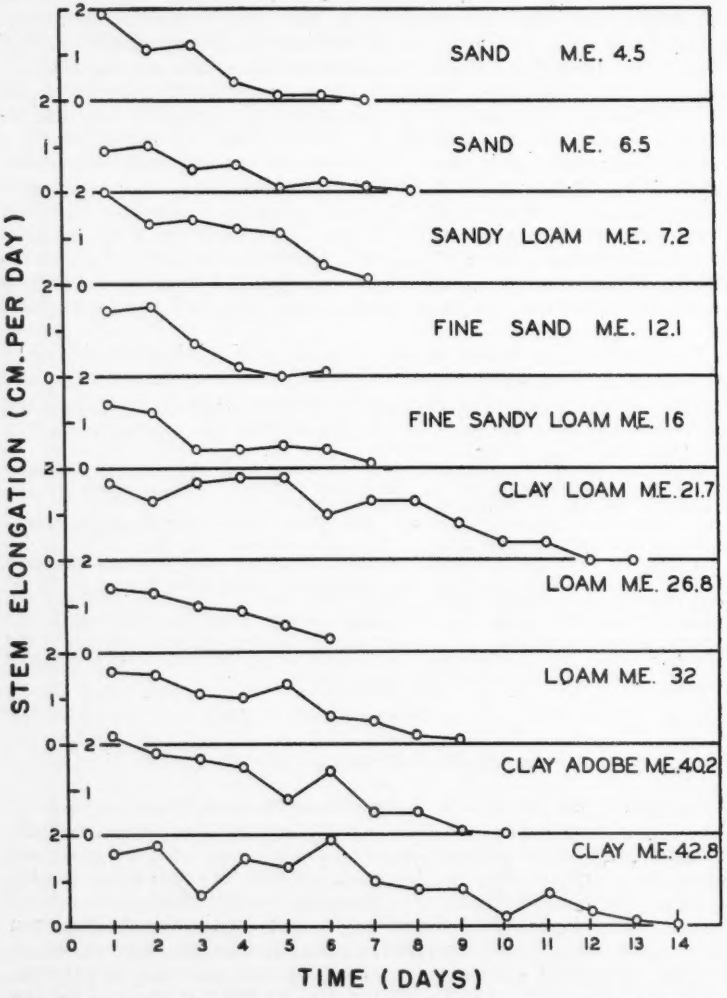
SAND M.E. 4.5
SAND M.E. 6.5
SANDY LOAM M.E. 7.2
FINE SAND M.E. 12.1
FINE SANDY LOAM ME. 16
CLAY LOAM M.E. 21.7
LOAM M.E. 26.8
LOAM ME. 32
CLAY ADOBE ME. 40.2
CLAY ME. 42.8
STEM ELONGATION (CM. PER DAY)
TIME (DAYS)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14

FIGURE 2.—Daily rate of stem elongation of sunflower plants in different soils accompanying decrease in soil moisture from field capacity (when growth measurements were begun) to first permanent wilting point (when last measurements were taken). Moisture equivalents (M. E.) given.

An attempt to estimate the changes in force exerted on water at the root surface during the progress of the decrease in moisture content of the soil from about the field capacity to the ultimate wilting point was made by determining the freezing point of samples of sap pressed from the plant tops and then calculating the equivalent osmotic pressure corresponding to the freezing-point depression. The plant tissue was kept frozen until just before the sap was extracted in a hydraulic press. Samples were taken from plants under two sets of conditions. One set of cultures was wetted to above field capacity and sampled at intervals as the soil dried out. The forces acting on the water in plant and soil were not brought to equilibrium by placing the cultures in a humid chamber; but the force gradient between plant and soil was comparable with that in the field at sunrise, since the

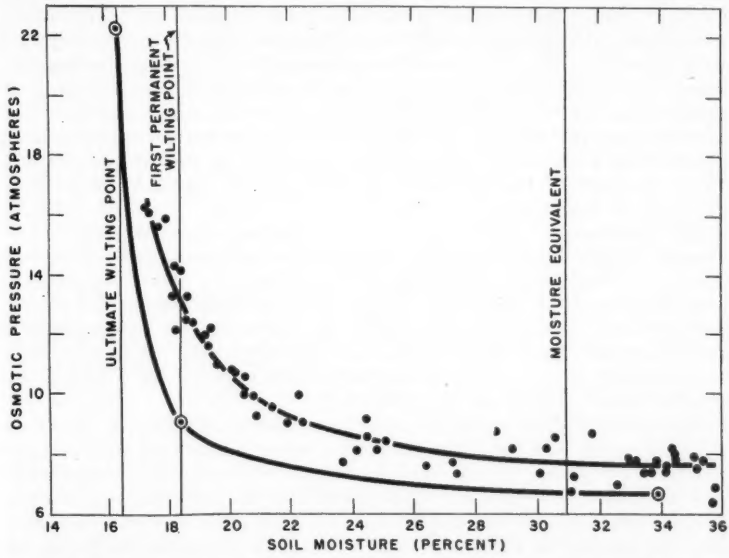

FIGURE 3.—Osmotic pressure of expressed sap from sunflower plants in soil at different soil-moisture percentages. Upper curve: Plants continuously in dry air; sampled at end of the dark period. Lower curve: Plants sampled after 16 to 24 hours in humid chamber.

plants were placed in a room overnight where the relative humidity was only slightly less than that of the outside air and then were sampled after a night of relatively low transpiration. The calculated osmotic pressure of samples of sap from these cultures is shown by the upper curve in figure 3.

These data (fig. 3, upper curve) show that as the moisture content of the soil decreased from about 24 percent to the lowest value reached, about 17 percent, there was a definite increase in the osmotic pressure of sap. Moisture determinations made on plant tops from these cultures showed that with decreasing soil moisture there was a concurrent decrease in moisture content of tissue. It is apparent that there

is a progressive change in the slope of the curve as the moisture content of the soil decreases below about 24 percent, but there is not a sharply defined break at 18.4 percent, the first permanent wilting point. At soil-moisture percentages several percent above the first permanent wilting point, the basal leaves of these plants failed to recover turgor during the night. It is clear that these plants, grown under atmospheric conditions resembling those in the field but with the roots rather uniformly distributed throughout a small mass of soil, were subjected to progressively increasing water deficit from a soil-moisture percentage about halfway between the moisture equivalent and the first permanent wilting point to a value below the latter.

The second set of cultures was sampled at only 3 different soil-moisture percentages. This set of cultures was divided into 3 groups. One group of 3 cultures was sampled at a soil-moisture percentage slightly above field capacity; another, of 17 cultures, at the first permanent wilting point; and a third, of 18 cultures, at the ultimate wilting point. The force gradient from plant to soil was presumably reduced to a very low value by placing these cultures in approximately saturated air for a period of 16 to 24 hours just before sampling. The cultures used for first permanent wilt were in the humid chamber most of the time for several days prior to sampling as well as for the last 16 to 24 hours. The cultures sampled at field capacity were presumably at full turgor.

The calculated osmotic pressures of the sap from plants at full turgor ranged from 6.4 to 6.8 atmospheres and averaged 6.6 atmospheres; at the first permanent wilting point the osmotic pressures ranged from 8.4 to 10.3 and averaged 9.1 atmospheres; and at the ultimate wilting point they ranged from 18.8 to 24.3 and averaged 22.2 atmospheres. The average values at full turgor, at the first permanent wilting point, and at the ultimate wilting point are shown as an assumed curve (lower curve) in figure 3.

The value of freezing-point determinations on expressed sap as an indirect measure of the forces acting on water at the root surface may be questioned, since the sap was extracted from the plant tops rather than from the roots and the wall pressure of the cells was not known. In spite of these apparent shortcomings, however, it seems probable that the method is fairly reliable. Water is translocated from one part of the plant to another so readily that apparently little difference in diffusion-pressure deficit exists in different parts of the plant unless transpiration is quite active (*2*, *9*). Therefore, there was probably very little difference between the diffusion-pressure deficits of tops and roots of the plants that were kept in the humid chamber most of the time for several days before sampling.

Under most conditions determinations of the osmotic pressure of expressed sap give no indication of the diffusion-pressure deficit of the tissues from which the sap was taken. In this instance, however, it may reasonably be assumed that at full turgor the wall pressure just equaled the osmotic pressure and that therefore the diffusion-pressure deficit was approximately zero. At the first permanent wilting point the wall pressure of the cells in the basal leaves was approximately zero, and the diffusion-pressure deficit was therefore approximately equal to the osmotic pressure. The diffusion-pressure deficit of the remainder of the plant top must have been equal to that of the lower

leaves and the osmotic pressure slightly higher than that of the basal leaves, since the upper leaves were at least partially turgid. It seems reasonable to assume that the diffusion-pressure deficit of the roots at the first permanent wilting point was somewhat, but not greatly, less than the osmotic pressure observed in the samples of sap expressed from the tops. At the ultimate wilting point wall pressure was probably zero, and the diffusion-pressure deficit was equivalent to the osmotic pressure. The marked increase in the osmotic pressure of sap, as the soil dried out from field capacity to the ultimate wilting point, undoubtedly resulted principally from loss of water by the tissue rather than from an increase in solutes. The average moisture content of plant tops, expressed as grams of water per gram of dry matter, was in plants at full turgor, 10.49; at the first permanent wilting point, 8.88; and at the ultimate wilting point, 5.24. The freezing-point determinations, then, indicate that the force with which water in soil at the root surface was held at the first permanent wilting point amounts to somewhat less than 9.1 atmospheres, and at the ultimate wilting point to about 22.2 atmospheres. These values, expressed in terms of soil-moisture tension, would indicate that, in soils practically free of salts, the tension at the first permanent wilting point may be somewhat less than 9,400 cm. of water (pF 3.97), and at the ultimate wilting point the tension may be about 22,900 cm. of water (pF 4.36).

From a comparison of the general level and change of slope of the curves in figure 3, it appears that at soil-moisture percentages between the moisture equivalent and the first permanent wilting point, the osmotic pressure of sap of the plants held in nonhumidified air was affected by transpiration. The state of turgor of leaves and the osmotic pressure of sap of these plants at soil moisture 2 or 3 percent above the first permanent wilting point were about the same as that of the plants from the humid air with soil moisture at the first permanent wilting point. When the soil moisture of both series of plants was at the first permanent wilting point, the difference in turgor and in osmotic pressure of sap of the two groups was quite large. With the decrease in soil moisture from field capacity to the first permanent wilting point, the increase in the osmotic pressure of the sap was about 5 atmospheres in the plants held in nonhumidified air but only 2.5 atmospheres in plants held in humid air. Apparently, when plants are held under conditions that permit water loss, even though the rate of loss is relatively low, as it was in this instance, there is some lag of absorption behind transpiration. At soil-moisture percentages near or in the wilting range the departure from equilibrium between the forces acting on the water in plant and soil may be large. Apparently, to obtain reliable values for the first permanent wilting point, it is essential that the cultures be handled in such a manner that the lower leaves just remain flaccid and that the second pair recover at least partial turgor when the forces acting on water in plant and soil are at approximate equilibrium.

When such conditions of equilibrium exist, the force with which water is held by soil at the root surface is, at the first permanent wilting point, probably nearly equal to the diffusion-pressure deficit of the basal leaves, and at this stage the turgor of cells in the growing regions has been reduced to the point at which further elongation does not take place or proceeds very slowly. First permanent, or irre-

versible, wilting is then a fairly well-defined stage in the progressive changes that occur in young healthy sunflower plants grown under certain specified conditions, and this stage is reached by all such plants in the same soil at approximately the same soil-moisture percentage. It should be clear, however, that the well-defined end point at the first permanent wilting point of the soil is well defined only so far as the response of the plant is concerned and only if the plant-soil system is at approximate equilibrium. The first permanent wilting point does not mark a point of abrupt change in the state or properties of the water in the soil. It has been supposed by some writers that there is a sharp break in the continuity of the water columns or films in the soil at the first permanent wilting point. Maximov (*11*, *p. 79*) suggested that ". . . even with the slowest rate of water absorption, the moment at last arrives when the water films in the drying soil are ruptured, and the water loses its mobility; this moment corresponds to the wilting coefficient." The fact that an appreciable amount of water is extracted by the plant at soil-moisture percentages between the first permanent wilting point and the ultimate wilting point indicates that there is not an abrupt cessation of water movement at the first permanent wilting point.

It is highly probable that root extension as well as stem elongation is negligible at soil-moisture percentages below the first permanent wilting point and that the extraction of moisture in the wilting range is dependent almost entirely on water movement to the roots. Diffusion of water vapor probably accounts for a part of this movement, but the results recently obtained by Richards (*13*) and Richards and Weaver (*14*) indicate that moisture transfer at rates higher than can be accounted for by gaseous diffusion occurs in soils at moisture percentages in the wilting range when pressures at the membrane surface are comparable in magnitude to the estimated diffusion-pressure deficits of roots in soil in the wilting range. Richards found that at a pressure of 16 atmospheres the moisture content of 5- to 10-mm. layers of soil was reduced from saturation to moisture percentages in the wilting range in 24 to 36 hours.

It has also been supposed that at the first permanent wilting point the force with which water is held by the drying soil increases so sharply that significant amounts of water cannot be extracted by the plant beyond this point, and that consequently the stage or degree of permanent wilting selected as the end point in wilting-point determinations is of slight importance. Vapor-pressure curves of soils are usually shown for a wide range of soil-moisture percentages, such as that from the moisture equivalent to the air-dry or oven-dry state, and over such a range the change in the slope of the curve appears sharp indeed in the region of the first permanent wilting point. It may be noted, however, from figure 3 that the break in the osmotic-pressure curve also is relatively sharp in the same region and that the increase of about 13 atmospheres in osmotic pressure, and presumably in diffusion-pressure deficit, between the first permanent wilting point and the ultimate wilting point results in the absorption of appreciable amounts of water at soil-moisture precentages below the first permanent wilting point, although it is true that below that point the rate of absorption is low.

WILTING RANGE AND ITS RELATION TO AVAILABLE RANGE, MOISTURE EQUIVALENT, AND PERCENTAGE OF SOIL COLLOIDS

The first permanent and the ultimate wilting points of the soils used in this study are shown plotted against the moisture equivalent in figure 4.

In general, the magnitude of the wilting range increases with increasing fineness of texture, as indicated by the moisture equivalent, but this relation is by no means consistent. Some soils of nearly the same moisture equivalent vary appreciably in magnitude of the wilting range.

The differences in magnitude of the wilting range are apparently largely determined by the moisture-retaining characteristics of the different soils at soil-moisture tensions in the wilting range, though

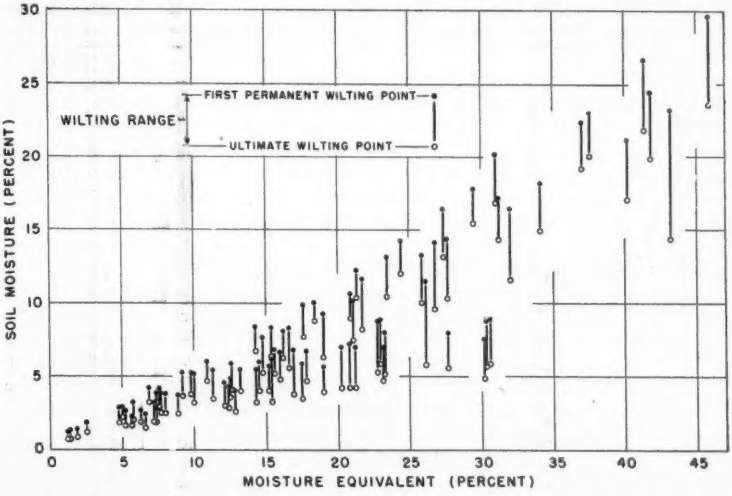

FIGURE 4.—First permanent wilting point and ultimate wilting point of different soils varying in texture from sands to clays. The wilting range of each soil is represented by the vertical distance between the first (dot) and ultimate wilting (open circle) points.

other factors, such as osmotic pressure of the soil solution, are probably involved. The moisture-retention characteristics have been determined on duplicate samples of many of these soils by Richards and Weaver (*14*). The slope of their moisture-retention curves at tensions in the region of the wilting range shows that, in general, for a unit change in tension the magnitude of the change in moisture percentage of the soil increases with increasing fineness of texture, but this relation, like that between wilting range and texture, is not consistent. That is, the moisture-retention curves of some soils of about the same moisture equivalent cross in the region of the wilting range.

The soil moisture within the wilting range provides the plant with an emergency reservoir that enables many species of plants to survive periods of prolonged drought or to mature seed after vegetative growth has ceased as a result of water shortage. With the reduction in the rate of absorption, which occurs near the first permanent wilting point, and the severe water shortage that follows, the various mechanisms by which transpiration is greatly reduced, such as stomatal closure and abscission of leaves, are set in motion; but after these changes are in progress there still remains the available water of the wilting range, which may be slowly absorbed over a relatively long period. Since the magnitude of the wilting range of different soils, even though they may be of similar texture, varies widely, it seems likely that this characteristic of a soil may be of some importance among those factors that effect the survival of plants during periods of drought. It is true, however, that the differences in magnitude

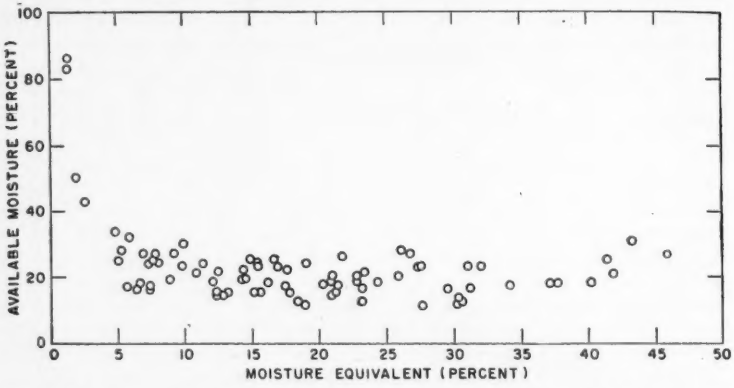

FIGURE 5.—Approximate percentage of available moisture held in wilting range of soils of different moisture equivalents.

of the wilting range of coarse- and fine-textured soils would be less, because of the greater volume weight of the coarse-textured soils, if the wilting range were expressed as moisture per unit volume of soil rather than as percentage of dry weight.

Perhaps the importance of the wilting range in the water economy of the plant may be evaluated most readily by a comparison of the wilting range and the range of soil moisture available to the plant. The approximate percentage of the available moisture that is held in the wilting range of soils of various moisture equivalents is shown in figure 5. The approximate available range is assumed to be the moisture held between the ultimate wilting point and the moisture equivalent. This assumption is not strictly correct, since the moisture equivalent is slightly higher in clays and appreciably lower in sands than the field capacity; but the moisture equivalent has been widely used as an approximation of field capacity, and, since it may be considered as a soil-moisture constant, determined by a standardized method, whereas the field capacity is not a constant but is affected by the peculiarities of the particular profile from which the sample

was taken, the moisture equivalent seemed to be a more suitable basis for a generalized comparison than the field capacity. It should be noted, however, that below a moisture equivalent of about 5 the discrepancy between the moisture equivalent and field capacity increases sharply; according to Browning (*7*), in soils of very coarse texture the field capacity may be two or more times the moisture equivalent. This, doubtless, accounts for the apparently high proportion of the available moisture held in the wilting range of the four soils of lowest moisture equivalent (fig. 5). Most soils of importance in agriculture fall within the textural range corresponding to moisture equivalents of 5 to 45, and in this range the proportion of the available moisture in the wilting range varies from about 11 to about 30 percent, averaging roughly 20 percent. It is clear that the proportion of the total available moisture that is held in the wilting range is great enough in most soils to be of significance in any consideration of the influence of soil-moisture shortage on the behavior of plants.

While it is not supposed that there is a sharply defined transition in the properties of the soil water or in the mechanism of water absorption by the plant at the first permanent wilting point or the ultimate wilting point, it seems possible to make a fairly well-defined division of soil moisture, so far as its availability to plants is concerned, into (1) that available for vegetative growth, (2) that available for maintenance of life under conditions of greatly reduced turgor, and (3) that unavailable to plants.

Because of the time and labor involved in making direct determinations of the wilting point of soils, several investigators have proposed less laborious, indirect methods, based upon physical measurements and not involving the growing of plants in the soil. The most widely used of these methods, that of Briggs and Shantz (*6*), is based upon an expected constancy of the ratio of the moisture equivalent to the first permanent wilting point, which they found to be approximately 1.84 in about 28 soil types investigated. Veihmeyer and Hendrickson (*18*) and, later, others called attention to the fact that in many soils the ratio of moisture equivalent to wilting point deviates widely from the value 1.84, observed by Briggs and Shantz.

Since the ratios reported by some workers (*18*) were nearly all above 1.84 and those reported by others (*15*) were nearly all below 1.84, it seemed possible that some of the variations in ratio observed may have resulted from variation in the degree of wilting judged by the different workers to be permanent wilting. In the present investigation, since the entire wilting range was determined, the possible importance of this factor may be evaluated from the data shown in figure 4. It is apparent from these data that wide variation in degree of permanent wilting could cause appreciable variation in the ratio of moisture equivalent to wilting point; but even the widest variation in this respect could account for only a part of the observed variability in ratio of these soils, since the ultimate wilting point of some lies far above the first permanent wilting point of others of about the same moisture equivalent. These data fully confirm the conclusion of Veihmeyer and Hendrickson (*18*) and others, that the ratio of the moisture equivalent to the wilting point of different soils varies widely. At first permanent wilt the moisture content of soils within the narrow

moisture-equivalent range of 30 to 31 varied from 7.6 to 20.2 percent and the ratio of the moisture equivalent to the first permanent wilting point varied from 3.97 to 1.53. The highest ratio of the moisture equivalent to the first permanent wilting point obtained in any of the soils (3.97) was obtained with a sample classified as Coachella fine sand, though it had moisture equivalent of 30.2 and mechanical analysis showed 30 percent silt and 40 percent colloid; whereas the lowest ratio, 1.08, was obtained with a coarse sand that had a moisture equivalent of 1.3 and was probably very low in percentage of colloid.

In an investigation of the relation of soil-moisture properties to texture in a large number of soils of the Okanagan Valley, British Columbia, Wilcox and Spilsbury (*20*) found that the values obtained for the wilting coefficient by the cohesion method of Bouyoucos (*5*) were closely correlated with the percentages of colloid as determined

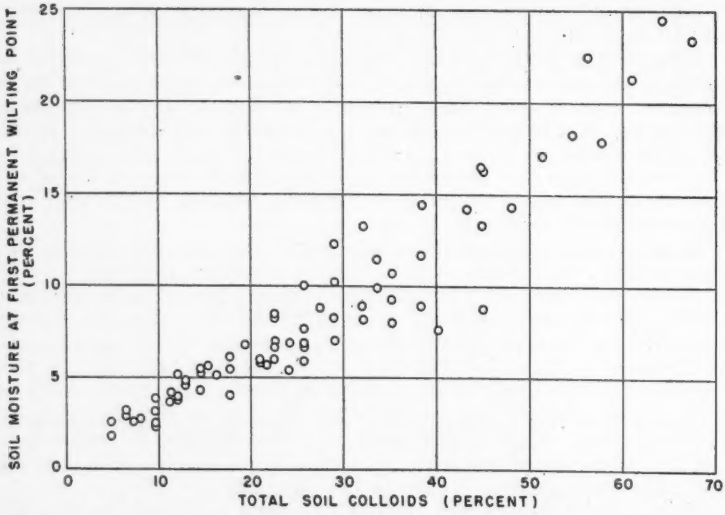

FIGURE 6.—Relation between percentage of soil colloids and first permanent wilting point of different soils.

by the hydrometer method of Bouyoucos (*4*). They concluded that the wilting coefficient may be calculated from the equation

$$\text{Wilting coefficient} = 0.12 \text{ percent colloid} + 1.338$$

with only a relatively small amount of error, though they warn that this equation may not prove satisfactory for use with soils formed under climatic conditions differing widely from those of the Okanagan Valley.

The relation of the first permanent wilting point to the percentage of colloids, as determined by the hydrometer method,[4] of most of the soils used in the present investigation, is shown in figure 6. It is obvious that the relation is not constant. For the 71 soils the average

[4] Thanks are due Dr. Walter Reuther, of the U. S. Date Garden, Indio, Calif., and James A. Cook, formerly of that garden, for the mechanical analysis of these soils.

ratio of percentage of colloids to first permanent wilting point was 3.21, but the ratios ranged from 1.85 to 5.29.

Although, in a general sense, with increasing fineness of texture there is an increase in the moisture equivalent, the percentage of colloids, and the wilting range, it is apparent that there are differences in the physical make-up of these soils that are not reflected in the moisture equivalent or the percentage of colloids.

A striking illustration of the failure of the moisture equivalent or percentage of colloids to reflect accurately the moisture-holding properties of the soil is that of several samples of soil from recent alluvial formations in the Coachella Valley, Calif. These soils are composed of 26 to 29 percent sand, 29 to 38 percent silt, and 32 to 45 percent colloids. The values for the first permanent wilting point range from 7.6 to 8.9 percent and for the moisture equivalent from 30.2 to 30.6 percent. It appears that, in relation to either the moisture equivalent or the percentage of colloids, these soils hold exceptionally low amounts of water at the first permanent wilting point.

It is possible that the movement of water through the soil to root surfaces, the number or distribution of roots, or perhaps the operation of other factors that might affect the value of the wilting points is related to variations in the texture and structure of the soil and in the composition of the soil solution; but it is highly probable that a large part of the variation in the ratios of the moisture equivalent or the percentage of colloids to the first permanent wilting point can be attributed to variations in the relative amounts of water retained by different soils with variations in soil-moisture tension. For example, the statement previously made regarding the moisture-holding properties of the Coachella Valley soils, as compared with others of similar moisture equivalent or percentage of colloids, may be generalized as follows: Soils A and B retain about the same amount of water at low moisture tension (moisture equivalent), while at high tension (wilting range) soil A retains less water than soil B.

Olmstead (*12*) found pronounced variations in the relative amounts of water retained by soils that had been saturated and then centrifuged in fields of 1,000 and 300,000 gravity, and more recently Richards and Weaver (*14*), using their porous-plate and pressure-membrane apparatus, found that the relative amounts of moisture retained by soils may vary over the entire range of moisture tensions from that at field capacity to that at the ultimate wilting point. Their curves showing the moisture retained by different soils at tensions ranging from about 2 to about 20,000 cm. of water are, however, more nearly parallel in the tension range above 3,000 cm. of water than in the range below this value. In their investigation, Richards and Weaver used duplicate samples of most of the soils employed in the present study. Their comparisons of the moisture percentage of these soils at a moisture tension equivalent to 15 atmospheres with the moisture percentages at the two wilting points suggest that the relation of the first permanent wilting point or of the ultimate wilting point to the 15-atmosphere percentage is more nearly constant than the relation of either of the wilting points to the moisture equivalent or to the percentage of colloids. The 15-atmosphere percentage would, therefore, probably serve as a more reliable basis for the indirect determination of the wilting range than would the moisture equivalent or the percentage of colloids.

DISCUSSION AND CONCLUSIONS

The idea that a soil has a relatively definite wilting coefficient, or first permanent wilting point, has been seriously questioned by various writers from time to time since Briggs and Shantz (*6*) first published the results of their work on this subject. Questions as to the reality of a first permanent wilting point have been raised, possibly as a result of a misunderstanding of (1) the meaning of the term "first permanent wilting point," (2) the precautions essential for the reliable determination of its value, and (3) the use to which it may be put in interpreting the behavior of plants in relation to soil-moisture conditions in the field.

The first permanent wilting point might be defined as that percentage of soil moisture at which the forces acting on the water in the soil are at approximate equilibrium with the forces acting on the water in a plant which is at that stage of turgor at which vegetative growth practically ceases. At moisture percentages above the first permanent wilting point, temporary wilting, or even death of much of the leaf surface, may result from prolonged exposure to conditions that produce intense transpiration. As long, however, as the moisture content of the soil is above the first permanent wilting point, vegetative growth of the plant may be resumed if transpiration is reduced to a negligible rate and other conditions are kept favorable for growth.

The results of the investigations of Caldwell (*8*) and of Shive and Livingston (*16*) have frequently been cited as proof that the moisture content of the soil at which permanent wilting takes place is affected by the environmental conditions existing during the wilting process. In the course of the present work, however, it was demonstrated many times that wilting plants rapidly or slowly made no significant difference in the soil-moisture percentage at first permanent wilt, provided the plants were placed in a humid chamber before the basal leaves were injured and before the second pair of leaves was permanently wilted. In the present investigation the plants were protected from rapid water loss after the first one or two temporary wiltings, because it was found that under conditions of low transpiration fewer transfers back and forth from the greenhouse bench to the humid chamber were required than if the plants were subjected to intense water loss. It seems possible that in reported instances of appreciable influence of the environment during wilting on the moisture content of the soil at permanent wilting the leaves may have been injured before the plants were placed in the humid chamber, that the degree of wilting may have been allowed to go beyond that of first permanent wilting before the plants were placed in the humid chamber, or that the roots may have been injured by high soil temperatures. Caldwell (*8*) reported root injury, which he attributed to desiccation, in some of his cultures. In the present work root injury, apparently resulting from high soil temperatures caused by exposure of several culture cans to direct sunlight on a hot day, was observed when the cultures were at soil-moisture percentages above the first permanent wilting point. Root injury that could be attributed to desiccation alone, however, was never observed in cultures dismantled

at the first permanent wilting point; and even at the ultimate wilting point most of the root system appeared to be alive.

The reality of a first permanent wilting point (wilting coefficient) of the soil has been questioned by some writers because soil-moisture conditions and wilting often appear not to be very closely related in the field. Soil within the root zone of plants in the field may be found to vary in moisture content from percentages well above the first permanent wilting point to percentages well below it; at the same time, depending upon the species and the weather conditions, some plants may show severe wilting and others no visible signs of water shortage. Wilting of a normal uninjured plant when the soil in the entire root zone is above the first permanent wilting point is temporary, and the plant may recover turgor and continue vegetative growth when transpiration becomes sufficiently reduced. On the other hand, it is not unusual to find under field conditions that the moisture content of the soil in a part of the root zone is below the first permanent wilting point before permanent wilting occurs and vegetative growth ceases. When temporary wilting occurs or a comparable state of turgor is reached in plants that do not show wilting, the diffusion-pressure deficit of the roots may soon become great enough to make possible absorption of water from soil at moisture percentages below the first permanent wilting point. This is likely to occur only in the zones of highest root concentration, while the soil in zones of lower root concentration is still above the first permanent wilting point. Then, when transpiration is greatly reduced, as at night, the plant may recover sufficient turgor, as a result of water absorbed by roots in soil at moisture percentages above the first permanent wilting point, to resume vegetative growth.

A prerequisite to the rational application of the conception of a wilting range of the soil to field conditions is an understanding of the manner and pattern of water extraction by the plant from the soil. From extensive field work relating to irrigation problems, there has been formulated the following picture of the typical pattern of root distribution and the sequence of events in the extraction of water from soil initially wet to soil at the ultimate wilting point. While the distribution of roots varies greatly with species and soil, the concentration of absorbing roots is typically greatest in the upper part of the root zone and near the base of the plant and decreases with soil depth or distance from the plant. Extraction of water is most rapid in zones of highest root concentration and most favorable conditions of temperature, aeration, and other environmental factors. When the moisture content in the zone of highest root concentration has been reduced to the first permanent wilting point, extraction in this zone does not cease, but the rate falls off sharply and the total water absorption rate of the plant decreases. As the total absorption rate and the turgor of the plant decrease, the diffusion-pressure deficit of the root system as a whole increases, the soil-moisture percentage is lowered into the wilting range progressively in zones of lower and lower root concentration, and, finally, as the severity of wilting increases, the soil-moisture percentage is reduced to the ultimate wilting point progressively from zones of highest root concentration to zones

of lower root concentration. By the time the plant in the field dies as a result of desiccation, the soil-moisture percentage in a large part of the root zone may have been reduced to the ultimate wilting point. Soil at the extremities of the root system, however, may still be well above the first permanent wilting point. The plant dies, not because water absorption has absolutely ceased, but because the rate of absorption finally lags too far behind the rate of loss to support life.

The significance of the first permanent wilting point or of the ultimate wilting point in the interpretation of field data lies in the fact that these points serve as reference values to which soil-moisture percentages may be related in making estimates of the amount of water in the root zone of a plant that is available for vegetative growth or for the maintenance of life.

It is hardly to be hoped that plant responses to soil-moisture conditions in the field may be very sharply defined. By the time the plant shows any visible effect of moisture shortage the moisture content of the soil in different parts of the root zone may vary widely; and atmospheric conditions, depth and distribution of roots, nutrition of the plant, the differences in susceptibility of different species to injury by temporary desiccation, and doubtless other factors affect the response of the plant in the field to soil-moisture conditions. By actual experiment with a given species of plant and set of soil conditions, however, it is possible to predict with a fair degree of accuracy the response that a plant will make when the moisture content of the soil in various proportions of the root zone is reduced to percentages in the wilting range under similar conditions of soil and climate.

SUMMARY

The range of soil-moisture percentages through which plants undergo permanent wilting has been termed the "wilting range of the soil." If the sunflower is used as the test plant, the upper end of this range, the first permanent wilting point, is marked by permanent wilting of the basal leaves, and the lower end of the range, the ultimate wilting point, is marked by complete permanent wilting of the apical leaves.

A standardized procedure for making wilting-range determinations is described, and the results obtained on about 80 soils are presented. At soil-moisture percentages near or in the wilting range even a low rate of water loss from the plant had an appreciable effect upon the osmotic pressure of the sap and upon the turgor of the plant. A decrease in soil moisture from field capacity to the first permanent wilting point caused, in plants in dry air, an increase of 5 atmospheres in the osmotic pressure of the sap and, in plants in humid air, an increase of only 2.5 atmospheres. The changes in osmotic pressure of plants in humid air indicate that the diffusion-pressure deficit of the plant was somewhat less than 9 atmospheres at the first permanent wilting point and about 22 atmospheres at the ultimate wilting point.

The proportion of the available moisture in the wilting range is great enough to be of considerable significance in investigations of the effect of soil-moisture shortage on plants. Of the moisture held between the ultimate wilting point and the moisture equivalent, the

proportion held within the wilting range of the soils investigated varied from about 11 percent to about 30 percent and averaged about 20 percent.

It was found, in agreement with other work, that the ratio of the moisture equivalent to the first permanent wilting point or to the ultimate wilting point is not constant. It was also found that the percentage of soil colloids, which has recently been used as a basis for calculation of the wilting point, would not serve as a reliable basis for calculation of the wilting points of the soils used in this study.

As related to plant behavior, soil moisture may be classified as (1) moisture available for vegetative growth, (2) moisture in the wilting range, and (3) moisture unavailable to plants.

In field work the first permanent wilting point and the ultimate wilting point may be used as reference values for estimating, respectively, (1) the amount of moisture in a soil that is available for vegetative growth and (2) the amount available for mere maintenance of life.

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TEMPERATURE IN RELATION TO DEVELOPMENT AND CONTROL OF BLUE MOLD (PERONOSPORA TABACINA) OF TOBACCO[1]

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INTRODUCTION

Blue mold, caused by *Peronospora tabacina* Adam, is known as a cool-weather disease of tobacco (*Nicotiana tabacum* L.). In Georgia it has been moderately active during periods with temperature between 30° and 35° F. Epidemic outbreaks, however, have usually occurred with minimum temperatures between 55° and 62°, and minimum temperatures between 65° and 70° have caused the disease to disappear. The inhibitory effects of only moderately high temperatures led the writers to study the feasibility of blue mold control through temperature regulation.

VIABILITY OF SPORES

To understand better the effect of temperature, it has been necessary to consider separately such important phases of disease activity as spore production, spore germination, and leaf infection. It is during the period of spore production that the most conspicuous stage of disease development occurs. After germination and infection have taken place, the mycelium grows through the leaf tissues for about 6 days without causing noticeable injury. The conidiophores then grow out through the stomata of the lower leaf surface about dawn, and within a few hours the affected leaf tissues begin to wilt and die. Obviously it was important to fix the period during which spores are mature and viable. This was done by selecting and marking, during the day, leaf lesions that had not yet sporulated but would probably sporulate the following morning. These lesions were then examined at intervals, and, after sporulation was first observed, germination tests were made from time to time. The results of such a test are given in table 1.

The data in table 1 show that only a few lesions had produced mature spores by 4 a. m. The majority of lesions had mature spores by 5 a. m., indicating the rapidity with which conidiophore growth and spore formation proceed. However, the fact that 7 of the 20 germination tests with spores collected at 5 a. m. gave values of 0 or 1 percent indicates that many of the spores were still immature. The highest mean germination was obtained with spores collected at 6 a. m. By 11 a. m. most of the spores were dead but 7 collections gave germination counts between 20 and 50 percent; and even as late as 5 p. m. a few of the spores were still viable.

[1] Received for publication Sept. 21, 1943. Cooperative investigation of the Division of Tobacco Investigations, Bureau of Plant Industry, Soils, and Agricultural Engineering, and the Georgia Coastal Plain Experiment Station.

TABLE 1.—*Maturity and viability of spores of Peronospora tabacina collected at different hours of the day*

Time collected	Collections with spores apparently in the condition indicated			Spores germinating in different collections	Spores germinating (mean)
	Mature	Immature	Not formed		
	Number	*Number*	*Number*	*Percent*	*Percent*
4 a. m.	1	4	15	0; 0; 9; 11; 24	9
5 a. m.	15	5	0	0; 0; 0; 0; 1; 1; 1; 10; 13; 15; 17; 36; 45; 47; 56; 56; 80; 81; 86; 93.	32
6 a. m.	16	4	0	3; 4; 4; 6; 7; 12; 21; 25; 35; 39; 47; 57; 80; 82; 85; 87; 88; 88; 91; 92.	48
8 a. m.	20	0	0	0; 0; 1; 4; 4; 4; 8; 11; 17; 21; 22; 29; 32; 33; 42; 68; 73; 74; 77; 83.	30
11 a. m.	20	0	0	0; 0; 0; 0.5; 1; 1; 1; 2; 2; 3; 3; 4; 12; 21; 21; 27; 31; 37; 40; 50.	13
5 p. m.	20	0	0	0; 0; 0; 0; 0; 1; 1; 1; 1; 1; 2; 2; 3; 4; 4; 4; 5; 5; 6; 7.	2

EFFECT OF TEMPERATURE ON SPORULATION

To obtain definite data on the relation of temperature to sporulation in the spring, leaves that appeared ready to sporulate were picked in the plant beds and held for 24 hours in a saturated atmosphere at different temperatures. In this preliminary experiment the leaves held at 40°, 50°, 69°, and 76° F. did not sporulate. A majority of those held at 64° and a lesser number of those held at 61° did sporulate. This result was surprising, because many temperature records made in plant beds have correlated heavy sporulation with a night temperature of about 60°. However, under natural conditions a night temperature minimum of 60° would be associated with a day temperature maximum of 75° to 80°. Tests were made, therefore, in which sporulation data at constant and alternating temperatures were compared.

The data in table 2 indicate that a temperature of 77° F. followed by 60° was more favorable for sporulation than 60° maintained continuously. No sporulation occurred when the temperature did not fall below 70°.

TABLE 2.—*Effect of constant and alternating temperatures on sporulation of Peronospora tabacina*

Temperature (°F.)	Exposure	Leaves sporulating	Average sporulation area
Constant temperature:	*Hours*	*Percent*	*Square inches*
50	24	12	0.16
60	24	35	.32
64	24	68	1.55
Alternating temperatures:			
77	7	32	.68
50	17		
77	7	79	3.38
60	17		
77	7	54	2.16
64	17		

When plants were grown in the greenhouse in winter under various temperature conditions and with high humidity, very different results were obtained. During January and February heavy sporulation occurred at 82.5° F. in one experiment and at 75° in two others.

Furthermore, the disease was repeatedly observed to develop freely in the greenhouse during midwinter with minimum temperatures of 70° to 80°, indicating that the temperature responses of the blue mold were not the same in the plant beds in the spring as in the greenhouse during the winter.

Study of this situation has led to the conclusion that these differences are related to light intensity. Bed-grown plants under the strong sunlight of spring had comparatively tough leaves, whereas plants grown in the greenhouse under the weak sunlight of winter had leaves that were tender and succulent. These winter plants were very much more disease-susceptible, and sporulation and disease development took place freely at minimum temperatures of 70° to 80° F. In the more resistant spring plants, sporulation and disease development did not occur at minimum temperatures in the 70° to 80° range. The fact that shading increases the severity of blue mold attack requires no proof, as it is a common observation that the shaded parts of plant beds are the most severely diseased. Furthermore, in parts that were shaded artificially the disease had remained active in the late spring for as much as 2 weeks after all development had ceased in adjacent unshaded parts of the bed. The effect of shading was also studied by growing plants under different thicknesses of cloth for different periods of time. Prolonged shading (3 to 4 weeks), which affected the type of growth, producing tender, succulent leaves, greatly increased sporulation and disease damage. However, growing plants in full sunlight, inoculating them, and then shading them for a week resulted in only a slight increase in disease development. The shading experiments were so arranged that differences in humidity were slight.

EFFECT OF TEMPERATURE ON SPORE GERMINATION

Germination tests with blue mold spores have given extremely variable results, as shown in table 1. This has raised the question as to what effect temperature might have on percentage of germination. Data are presented in table 3 on spore collections made at different hours on two different days.

TABLE 3.—*Effect of temperature on spore germination of Peronospora tabacina*

Spore series and time of collection	Germination at indicated temperature (° F.)												Optimum germination temperature
	35	40	50	60	63	64	69	71	73	77	79	82	
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	° *F.*
Series 1:													
5 a. m.	0	2	33	7	.....	23	.....	49	72	.....	30	8	73
6:30 a. m.	20	15	7	4	.....	13	.....	55	84	.....	21	19	73
8 a. m.	16	21	19	10	.....	90	.....	60	30	.....	80	17	64
9:30 a. m.	21	14	11	19	.....	30	.....	39	11	.....	41	2	79
11 a. m.	5	18	26	10	.....	33	.....	.....	16	.....	9	3	64
Series 2:													
6 a. m.	95	95	95	9	10	.....	2	.....	60	2	.....	.....	35–50
7:30 a. m.	98	98	95	50	23	.....	27	.....	19	25	.....	.....	35–40
9 a. m.	37	46	84	12	13	.....	9	.....	21	16	.....	.....	50
11 a. m.	50	97	98	44	27	.....	13	.....	73	84	.....	.....	50
2:30 p. m.	48	33	95	40	5	.....	8	.....	2	8	.....	.....	50

The data in table 3 offer some interesting contrasts. It is evident that the same spore collection gave widely different germination percentages at different temperatures. Thus, in the series 1, 6:30 a. m. collection there was 7 percent germination at 50° F. and 84 percent at 73°. On the other hand, in the series 2, 6 a. m. collection there was 95 percent germination at 50° and 60 percent at 73°. There was no consistent optimum temperature for spore germination, and the optimum for each separate collection is listed in the last column of table 3. In series 1 optimum values ranged from 64° to 79° and in series 2 from 35° to 50°. Thus, there was variability in the responses of collections made on the same day and a complete shift in the temperature responses of collections made on two different days. Further germination tests were made on five other series of spore collections, each on a separate day, conducted in the same manner as those reported in table 3. In three series, germination was favored by cool temperatures (35°–50°), and in two by warm temperatures (64°–79°). In no experiment was any germination of spores obtained with temperatures of 85° or above.

Many factors besides temperature during germination affect the viability of spores. The spores produced on young seedlings (3 to 4 weeks old) have generally germinated much more poorly than spores produced on the leaves of plants 6 to 8 weeks old. Moreover, the temperature conditions that prevail while spores are being formed may have a marked effect on spore viability. Germination tests were made on spores produced under the different temperature conditions indicated in table 2, and the results were as follows: Maximum germination (94 percent) was obtained with spores produced at a temperature of 77° F. by day and 60° by night, whereas minimum germination (less than 1 percent) was obtained with spores produced at 50° maintained continuously. In general, abundant spore production has been associated with high viability.

Temperature is also a factor in determining the longevity of spores. Experiments were conducted in which the spores were stored in a saturated atmosphere at different temperatures. As would be expected the results showed that spores held at the cooler temperatures (35° and 40° F.) survived the longest. Actual freezing did not prove harmful; freshly sporulating leaves were held for 9 days at 16°, and the spores removed at the end of that time germinated about 70 percent as well as the spores of the same collection did originally. Spores stored at 32° did not keep nearly so well as those stored at 16°. The ability of the spores to live for days in a frozen condition was reported by Angell and Hill (*2*),[2] and this ability may have been an important factor in the recent spread of blue mold from the western to the eastern part of the United States.

EFFECT OF TEMPERATURE ON PLANT INFECTION

To obtain infection data, tobacco plants were sprayed with a suspension of spores in the early morning and then held in a saturated atmosphere at different temperatures for 24 to 72 hours. After this, they were removed to an open greenhouse where conditions favored disease development. Notes were taken at the end of 9 days, i. e.,

[2] Italic numbers in parentheses refer to Literature Cited, p. 182.

before secondary infection had become a factor. No experiment was made to determine whether temperatures at the time of inoculation affected the latent period, or length of time required for symptoms to appear. Figure 1 shows typical results. Incubation at 35°, 40°, 50°,

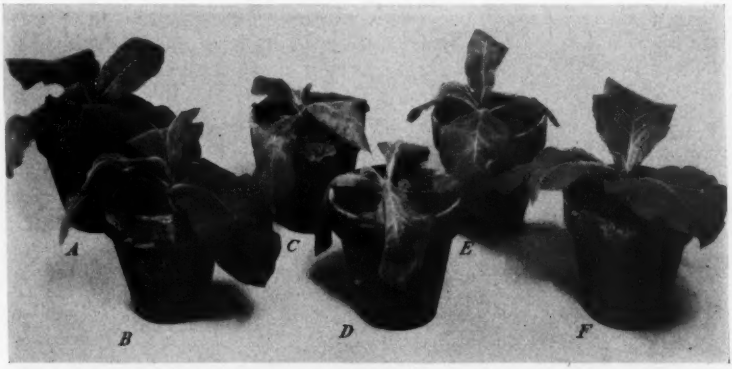

FIGURE 1.—Temperature in relation to blue mold infection. Plants were inoculated and then incubated for 48 hours at the following temperatures: *A*, 40° F.; *B*, 50°; *C*, 64°; *D*, 75°; *E*, 80°; *F*, 90°. Temperatures of 64° and 75° favored disease development.

and even 60° F. resulted in slight disease development; at 64°, 70°, and 75°, infection was severe. No disease development was obtained after incubation at 85° or more, though abortive lesions were observed. In several of these experiments, it was possible in the early stages of disease development to count separate lesions. Such counts showed the following number of lesions per plant: With incubation at 35° and 40°, no lesions; at 50° and 62°, 14 to 16 lesions; at 64° and 70°, 25 to 35 lesions; at 74° and 77°, 85 to 89 lesions. Infection thus was favored by temperatures distinctly higher than the temperatures favoring spore production.

CONTROL BY TEMPERATURE REGULATION

During the 5-year period from 1933 to 1937, inclusive, experiments were conducted each year, principally at Tifton, Ga., and at the Arlington Experiment Farm, Arlington, Va., with plant-bed units so arranged as to provide various minimum night temperatures. Electric heating cables with thermostats were used to obtain uniform gradations of night temperatures. During the day temperatures were not regulated.

Table 4 shows a representative set of data.

TABLE 4.—*Control of blue mold in the plant bed by temperature regulation at night*

Minimum night temperature (°F.)	Sporulating leaves on 250 plants	General condition of plants
	Number	
60–64	650	Defoliation complete.
65–69	300	Defoliation moderate.
70–74	1–	Trace of infection.
75–79	1–	Do.
Check (55–63)	566	Defoliation complete.

The temperatures in the check areas dropped to 55° F. on some nights, and the disease was actually less active than in the 60° to 64° plots. Disease development decreased with 65° to 69° and was almost completely inhibited at 70° to 74° and at 75° to 79° (fig. 2). Humidity

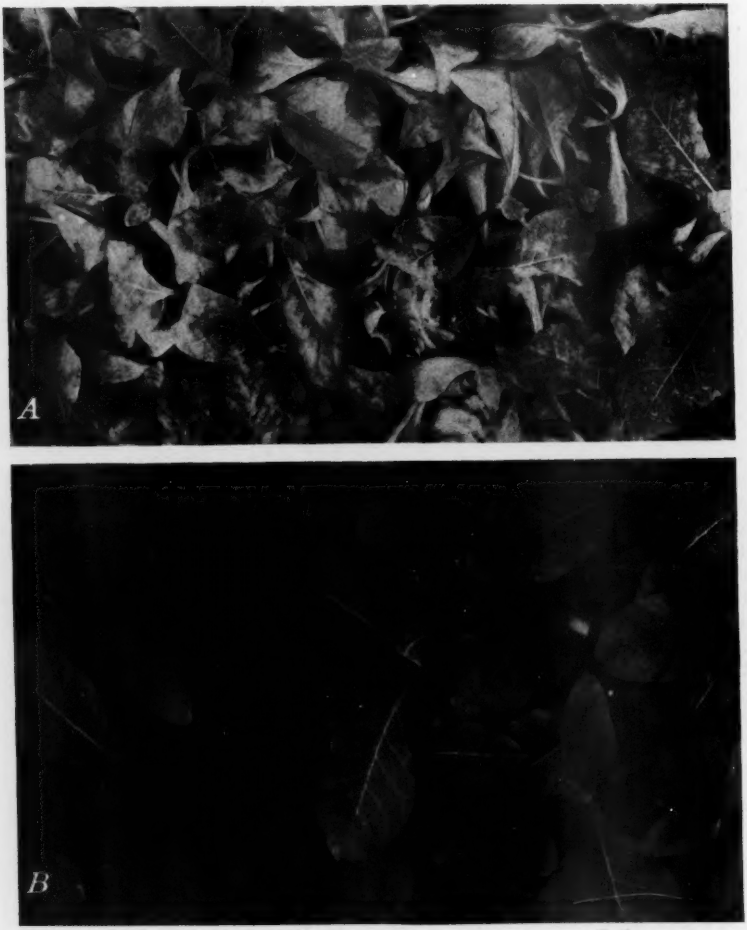

FIGURE 2.—Blue mold control by temperature regulation: *A*, Nonheated check; *B*, a section heated at night to maintain the temperature above 70° F. Severe blue mold developed in section *A*, while the plants in section *B* remained healthy.

reached saturation each night except with the very highest temperature.

In the work at Tifton, Ga., particular attention was paid to the development of practical plant-bed equipment for heat treatments. It was found that, because of the costs of installation and current,

electricity would be too expensive for the average tobacco grower. Figure 3 shows a flue-heated bed in which excellent blue mold control was obtained. The heat was provided by wood or coal fires, and the bed was covered with heavy muslin. Of the various heating methods tested, however, small oil heaters were found to be the most practical.

The fact that blue mold was regularly and effectively controlled in spring plant beds by maintaining night temperatures above 70° F., whereas the same treatment was completely ineffective in the greenhouse in midwinter, raised the question as to what would be the reaction of plants grown in beds sown in the autumn. In spring-sown plant beds, disease activity is checked abruptly by the first hot days of summer. However, when seed is sown about August 20 in the vicinity of Washington, D. C., blue mold becomes active about September 20

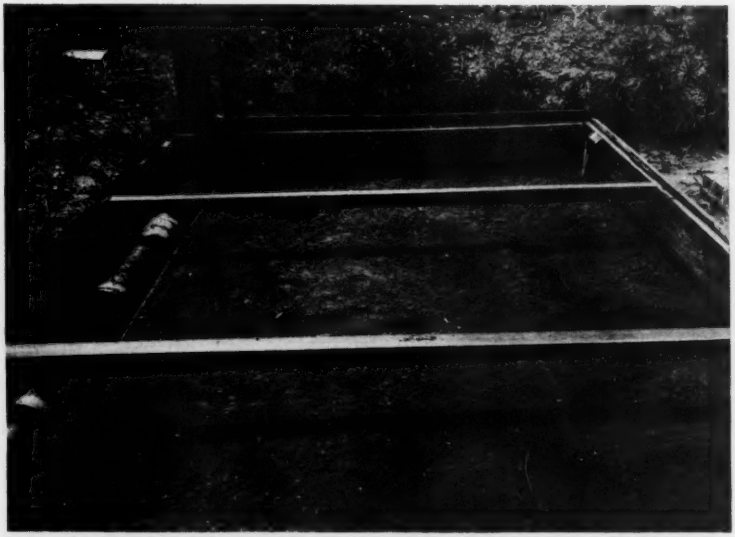

FIGURE 3.—A flue-heated tobacco plant bed. Excellent blue mold control was obtained in this bed in 1933.

After October 10 disease activity diminishes as temperatures drop. In the spring as plants grow the temperatures rise and the sun gets brighter, whereas in the autumn this sequence is reversed.

The first year that beds were sown in the autumn and temperature controls were established, September was warm and sunny. The plants resembled those grown in spring, and they reacted in the same manner to blue mold; that is, when the minimum night temperature was maintained above 70° F., effective blue mold control resulted. The autumn of the following year (1934) was very different. September was the wettest on record; and, owing to this excessive moisture and the cloudy weather, plant growth was succulent and soft. In this experiment there was abundant disease development at a night minimum of 70° to 75°, and the disease was almost equally active throughout the entire range of 60° to 75°. However, when the temperature

was raised to 85° to 90°, all disease development was promptly checked. To summarize briefly: In the spring sporulation is inhibited by night temperatures above 70°; in the autumn sporulation may or may not be inhibited by temperatures above 70°; and during the winter sporulation proceeds freely with night temperatures as high as 80°.

In studying the value of short treatments at temperatures above 85°, it seemed evident that such treatments would be most practicable during the day, when the heat of the sun would be an aid. The treatment periods, consequently, were limited to the period from 9 a. m. to 4 p. m. Except during the actual treatment period, the test plants were constantly exposed to reinfection and were held at temperatures favorable for blue mold development. The results from a number of tests are summarized in table 5.

TABLE 5.—*Control of blue mold by short treatments at high temperature*

Temperature (°F.)	Exposure per week	Blue mold development	Temperature (° F.)	Exposure per week	Blue mold development
	Hours			*Hours*	
90	12	Severe.	110	2	Moderate.
90	16	Do.	110	4	Slight.
90	48	Moderate.	110	8	Trace.
100	4	Do.	110	12	None.
100	8	Do.	Check		Severe to very severe.
100	12	Slight.			

In table 5 disease development designated as slight or less indicates practically perfect disease control, as figure 4 shows. Four hours per week at 110° F. effectively controlled blue mold, while a reduction of the temperature to 100° increased the time required for treatment to 12 hours. These results were obtained under severe disease conditions. In several experiments, 2 hours' treatment per week at 110° controlled

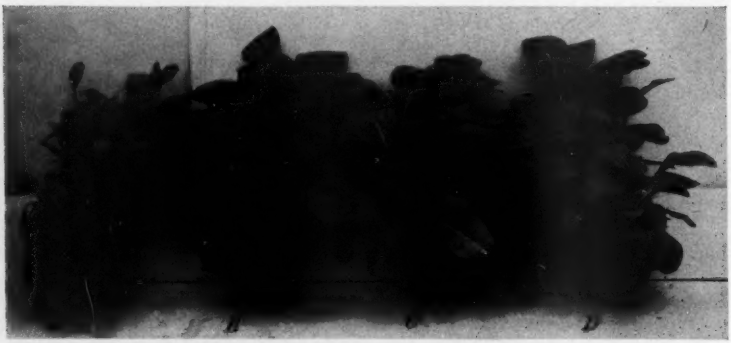

FIGURE 4.—Control of blue mold by short treatments at high temperatures: *A*, Untreated check, severe blue mold; *B*, 2 hours per week at 110° F., slight blue mold; *C*, 4 hours per week at 110°, no blue mold; *D*, 8 hours per week at 110°, no blue mold. Except during the brief treatment periods, plants were held under conditions favoring blue mold development and were constantly exposed to reinfection.

blue mold, but under the most severe conditions 4 hours were required. High-temperature heat treatment has been successfully used in large greenhouse units. The procedure there was to select a bright day and to leave the heat on and the ventilators closed. In the early spring it was possible to hold temperatures between 105° and 110° from 10 a. m. to 3 p. m., and such a treatment once a week has given very effective blue mold control.

High-temperature treatment was also used with success in cold frames with a large air capacity, but it did not prove safe in the usual sash bed because the very limited air space caused rapid fluctuation in temperature. Unless plants were extremely succulent, the only injury caused by 110° F. was a slight retarding of growth.

The high-temperature method did not prove practicable in regular commercial beds during the normal plant-bed season in Georgia, and effective control was obtained only in small tight beds covered with glass or glass substitutes. Heavy canvas covers were not suitable. It was not feasible to maintain the required uniformly high temperature on cold, windy, or cloudy days. Since very severe blue mold infection has occurred in Georgia during the coldest part of the winter, this treatment could be depended upon only during bright spring days or late in the plant-bed season. At such times the disease has not been very destructive and control was less essential than earlier in the season.

DISCUSSION

Pathologists generally have found rather definite and narrowly limited optimum temperatures for both the germination of fungus spores and the development of disease. The present studies show, however, that the optimum temperature for germination of *Peronospora tabacina* spores varied greatly with different collections. With some collections of spores the most favorable germination temperatures were 35° to 50° F., and with others 64° to 79°. No germination of spores was obtained at 85° or above, nor at 32° or below; so it is quite apparent that the optimum range was only a little less wide than the total range over which germination occurs.

The situation with respect to blue mold control by temperature regulation is also unusual. The writers reported (*4*) inhibition of sporulation and excellent control of blue mold by maintaining night temperatures above 70° F. These experiments were carried out in the usual spring plant beds and confirmed observations made by other workers (*1*, *5*) that little if any sporulation occurs at temperatures above 68°. In fact, it is usual in the spring for the disease to disappear after a few nights with minimum temperatures between 65° and 70°. However, Armstrong and Sumner (*3*) reported sporulation with temperatures that remained above 80°, and in the experiments reported here the writers have found that blue mold can develop freely at a minimum temperature of 70° to 80° and produce spores abundantly as well. The essential condition for this high-temperature disease activity has been vigorous growth of the tobacco plants coupled with low light intensity, which results in very tender and succulent foliage. Thus, depending on the condition of the host plant, sporulation and disease development may or may not be inhibited by temperatures between 70° and 80°. Over a 5-year period (1933–37) the writers did not fail to obtain excellent blue mold control in repeated

tests by maintaining night temperatures above 70°. These experiments were all conducted in the usual spring plant beds. Experiments were also conducted in autumn-sown plant beds, and during 1 year, with September dry and bright, perfect blue mold control was obtained by maintaining night temperatures above 70°. The following year, September was very cloudy and sporulation and disease development proceeded freely at night temperatures of 70° to 75°. In midwinter in the greenhouse, the disease is very active at minimum temperatures of 70° to 80°. The statement that maintaining a minimum temperature above 70° will stop sporulation and control blue mold appears to be consistently true under usual plant-bed conditions in the spring, but it is not true in the greenhouse in midwinter.

A further illustration of the effect of the physiology of the plant on the temperature relations of the disease is the situation in New England, where tobacco grown under artificial shade sometimes is damaged severely by blue mold while the field crop grown without shade is at most very slightly affected.

It is of interest to note that temperatures during the day affect spore production the following night. It is usually considered that night temperatures of 55° to 60° F. favor sporulation, but table 2 shows that an alternation of higher and lower temperatures was much more favorable for sporulation than a uniform lower temperature.

It should be pointed out that in most of these studies temperatures were kept fairly constant, whereas under actual plant-bed conditions temperatures usually fluctuate constantly and vary widely. The fact that a maximum of 77° F. and a minimum of 60° were more favorable for sporulation than a constant temperature suggests the possibility that more frequent and wider fluctuations might have still greater influence and that such variation might have an important bearing on spore germination, infection, and subsequent disease development. Since the optimum temperature for germination of spores collected in these experiments varied from 35° to 79°, it is evident that all the factors governing viable spore production and germination are not yet understood. In the controlled experiments here reported sporulation did not occur at temperatures below 50°, yet in commercial plant beds in Georgia sporulation has occurred freely on mornings when the plant-bed cover was coated with frost and temperatures inside the bed remained below 50° all night and well into the forenoon.

Finally, it may be noted that disease development in these tests proceeded most rapidly when night temperatures remained between 55° and 62° F., but this maximum rate of development usually was confined to a few days near the end of the epidemic. When blue mold is very destructive in Georgia most of the damage occurs during long, cool periods with night temperatures between 30° and 50° and with wide ranges between maximum and minimum temperature. Blue mold has been observed to remain active during the coldest periods tolerated by tobacco plants. Disease activity is slower during such periods, but the total damage is very great.

These studies have made it possible to operate a blue mold resistance breeding program without interruption throughout the summer. To do this a large insulated chamber was constructed and adjusted to give a day temperature of 75° F. and a night temperature of 60°.

Light was provided by fluorescent tubes. Plants were inoculated and held under these conditions for 96 hours. They were then moved to a bed located in a shaded, well-protected area, with muslin covers to provide additional shade as required. Under these conditions blue mold development was uniform and severe during the hottest weather of August. Luxuriant sporulation took place the sixth and seventh mornings after inoculation, and 14 days after inoculation 70 to 95 percent of the plants were dead. In a few days more, mortality was frequently 98 to 100 percent. This serves to emphasize again the fact that, although blue mold is a cool-weather disease, some phases of its development are greatly favored by moderately high temperatures provided light is controlled.

One of the numerous puzzling problems with respect to blue mold has been the report from Bathurst, Australia (*7*), of effective blue mold control for 12 consecutive years by growing plants in flue-heated beds. This control was attributed to the maintenance of temperatures above 45° F. Hill and Allan (*6*) later found that this treatment was ineffective, as would be expected, since the disease is recognized to be most active at minimum temperatures between 40° and 60°. However, in the Bathurst report reference is made to temperatures as high as 110°, and it is stated that even 125° to 130° caused no harm if the plants were not tender. The writers' studies have shown that excellent blue mold control can be obtained with exposure for 4 hours per week at 110° and that even 2 hours per week is rather effective. In view of the potency of high-temperature treatment, it appears that at Bathurst, where the method of heating permitted wide fluctuations, the actual blue mold control achieved was the result of occasional high temperatures and not of the maintenance of temperatures above 45°.

The effectiveness of high temperature in destroying the fungus was not modified by the condition of the host plant. However, the ability of the plant to withstand high-temperature treatment was much affected by the succulence of the tissues. Very tender plants can be severely injured by treatment at 110° to 115° F. High-temperature treatment worked especially well in greenhouses, where the large volume of air and the comparative ease of temperature regulation make blue mold control by this method quite simple.

In general, temperature control of blue mold in the plant bed, either by all-night treatment with temperatures held above 70° F. or by short treatments at 110°, is not likely to be used widely because gas and spray treatments that are available are effective and less expensive. However, a shortage of materials for gas or spray treatment might well result in the use of heat treatment for blue mold control.

SUMMARY

The spores of *Peronospora tabacina* are produced in the early morning and die within a few hours unless infection occurs.

Viability of spores was affected by the temperature conditions both at the time of spore formation and at germination.

Sporulation was most abundant with a night temperature of 60° F. preceded by a higher day temperature.

Some collections of spores germinated best at cool temperatures (35°–50° F.) and other collections at warm temperatures (64°–79°); hence a single optimum temperature for spore germination does not exist.

Leaf infection was favored by temperatures of 64° to 75° F., and germination and infection were both inhibited by temperatures above 85°.

Almost no sporulation occurred in tobacco plant beds with minimum night temperatures of 70° F. and above. Maintenance of such temperatures by artificial heating gave consistent and highly effective control of blue mold.

Plants grown with reduced light, as the result of heavy shading or midwinter conditions in the greenhouse, sporulated freely with minimum temperatures as high as 80° F.; hence, under such conditions, temperature control based on inhibition of sporulation was not practicable.

The lethal effect of temperatures above 85° F. on the fungus was not modified by the condition of the host plant. Exposure to 110° for 4 hours per week controlled blue mold effectively in plants that between treatments were constantly exposed to reinfection. In the greenhouse, exposure of the plants for 5 hours per week to a temperature of 105° to 110°, using heat from the sun, gave complete control of blue mold.

Heat treatment for the control of blue mold was generally more expensive than either spray or gas treatment.

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